# THE RESPECTIVE INFLUENCES OF TEMPERATURE AND MOISTURE UPON THE SURVIVAL OF THE RAT FLEA (*XENOPSYLLA CHEOPIS*) AWAY FROM ITS HOST[1].

By A. W. BACOT and C. J. MARTIN.

(*From the Lister Institute, London.*)

(With 3 Text-figures.)

The rapid fall in the number of plague cases with the onset of hot weather is a characteristic feature of plague epidemics in the northern half of India. In these regions the rise in temperature is accompanied by an increased drying capacity of the atmosphere so that it is impossible to assess to what extent the higher temperature and increased drying power are respectively responsible for the effect.

Epidemiological observations made in Mauritius (1899), Southern India (1908) and Java (1914) suggest that a rise of temperature, without increased drying power of the air, restrains plague epidemics. These observations have been ably analysed by Brooks (1917). The object of the experiments set forth below was to ascertain the separate influences of temperature and drying upon the longevity of fleas with a view to the interpretation of the epidemiological facts.

To save possibility of confusion we may be permitted to point out that the meteorological term relative humidity does not indicate the drying capacity of an atmosphere. Drying power depends on the saturation deficiency, that is the extent to which the vapour pressure of water in the air is short of the saturation pressure for the particular temperature. Investigation both by members of the Plague Commission in India (1912) and by Bacot (1914) in this country have shown that considerable saturation deficiency exerts an inimical influence at almost every stage of the life history of the insect and the consequent diminution in flea-population no doubt plays a considerable part in modifying the spread of plague. Our observations are only concerned with the effect upon the longevity of the adult insect apart from its host.

Whilst living amongst the fur of an animal the insect is exposed to a nearly constant climate. Also, it can slake its thirst whenever it is so disposed. Once separated from its host, however, the time which elapses before its career is ended by desiccation is principally determined by the drying power of the atmosphere. This is abundantly illustrated by the experiments in the reports referred to above and also by the observations of Nicoll (1912) and of Petrie (1923) in Egypt.

Apart from the general reduction in flea population, saturation deficiency

[1] The experiments recorded in this paper were made in 1914. The work was put aside during the war. For various reasons, amongst them the death of Arthur Bacot, who contracted typhus whilst experimenting with infected lice, the observations have not been recorded until now.

has a special significance in the epidemiology of plague, for when a rat dies of plague its fleas have, perforce, to roam in search of another host and the longer the time vouchsafed to them, the greater the chances of a successful quest.

The time of survival is abbreviated in the case of fleas in which the lower end of the gullet is obstructed by cultures of plague bacilli. Such fleas are particularly sensitive to climatic conditions as they may be already a bit dehydrated. Although they bite continuously they find great difficulty in satisfying their thirst. The action of the pharyngeal pump distends the oesophagus with blood but little or none enters the stomach and on the pump ceasing to function the blood flows back into the wound carrying with it plague bacilli from an infected gullet. We have shown elsewhere (1914) that insects in this condition are principally responsible for the transmission of infection from rat to rat and presumably from rat to man. We could, however, keep fleas alive for weeks when the entrance to the stomach was completely blocked if the atmosphere were nearly saturated and the temperature below 5°.

The Poona observers attempted to answer the question whether temperature, apart from humidity, exerted any direct influence upon the length of life of fleas, by reducing the latter to nothing. They kept fleas at different temperatures in test-tubes in which the air was dried by calcium chloride and found that at 101° F. the mean duration of life was 0·14 day whereas at room temperature (55–85° F.) it was 1·17 days and in a cool box at 60° F. it was 1·66 days. The influence of temperature could hardly be arrived at in such a manner, for, assuming the air in the tubes to have been dry, the saturation deficiency was different at each temperature. It would be 50 mm. at 101° F., 18·7 mm. at 70° F., and 13·6 mm. at 60° F. In addition to changing the temperature of the fleas the observers had unintentionally varied the drying power of the atmosphere to the maximum extent.

What we set out to do was (1) to keep the saturation deficiency constant while temperature was varied, (2) to keep temperature constant while saturation deficiency was varied and so determine the effect of each of these variables upon the longevity of the insects.

## Methods employed.

The most convenient way of arranging atmospheres having the same temperature but different saturation deficiencies or the same saturation deficiency but different temperatures is to bring them into equilibrium with various mixtures of sulphuric acid and water. If, for instance, air is slowly bubbled through water at 10° C., it takes up water to the maximum vapour pressure for that temperature, viz. 9·2 mm. If it is bubbled through pure $H_2SO_4$ its vapour pressure is reduced to zero. By arranging the proportion of acid to water in the mixture through which the air is passed, any intermediate vapour pressure can be arrived at.

From Regnault's data which are given in Landolt and Börnstein's tables (1905 edition, p. 166) the mixture required to give a particular vapour pressure at a particular temperature can be calculated. This is the procedure we adopted. The fleas were in a bottle which was maintained at a constant temperature through which a constant stream of air of the same temperature and the desired saturation deficiency was drawn.

One hundred fleas from the breeding cage were placed in small test tubes about an inch long, ten fleas to each tube. The tubes were covered with gauze and suspended in a cage inside a wide-necked bottle of about 700 c.c. capacity. At the bottom of the bottle was 200 c.c. of a mixture of sulphuric acid and water in the required proportion. The neck of the bottle was closed with a rubber bung penetrated by two glass tubes, one of which dipped beneath the acid. Air was drawn through the bottle, bubbling through the sulphuric acid mixture. As merely bubbling through a couple of inches would not bring the vapour pressure in the air into equilibrium with that of the mixture of sulphuric acid and water, the air was passed through two other gas-washing bottles containing the same strength of sulphuric acid at the same temperature before entering the bottle containing the fleas. This, we ascertained, sufficed to obviate change in the concentration of acid in the final bottle. A constant temperature was secured by immersing the whole apparatus in a large water bath controlled in the usual way. The bottle was examined twice daily. The dead fleas were counted and removed and the bottle replaced in the bath.

The fleas used in the experiments were *Xenopsylla cheopis* bred in the laboratory. They were taken from the breeding cages immediately before use and represented a mixed population of various ages and in different states of nutrition.

We employed throughout a flow of 100 c.c. per minute. The details of the procedure for controlling saturation deficiency and temperature will be grasped from an example. Supposing it were desired to subject the fleas to a current of air of 100 c.c. per minute at the temperature 32° C. and with a saturation deficiency of 10 mm. mercury pressure, *i.e.* a vapour pressure of 25·6 mm.

The saturation vapour pressure at 32° C. is 35·6 mm. 35·6 − 10 = 25·6 mm. 32 per cent. $H_2SO_4$ solution at 32° C. has a vapour pressure of 25·6 and air brought into equilibrium with acid of this strength will have this vapour pressure and, *as long as it be maintained at* 32° C., a saturation deficiency of 10 mm.

Air was passed firstly, through a gas-washing bottle containing water, immersed in a bath at 27° C. The vapour pressure at 27° C. is 25·6 mm. and the issuing air had a vapour pressure of about 25 mm. For the final adjustment of its vapour pressure, it was driven through two gas-washing bottles containing 32 per cent. $H_2SO_4$ and thence into the bottle containing the fleas, bubbling through more 32 per cent. $H_2SO_4$ in the bottom of this bottle. These last two gas-washing bottles and the bottle containing the fleas were immersed in a bath at 32° C. The various bottles were connected by short lengths of

rubber tube. To secure a constant stream of 100 c.c. per minute, the air was delivered at constant pressure by means of an overflow valve through a gas meter. The flow was adjusted by regulating the resistance.

## PRELIMINARY TEST OF APPARATUS.

Within the range of temperature we are considering, air with the same saturation deficiency and the same movement dries an object at very nearly the same rate, whatever the temperature. There is a small advantage at the higher temperature because molecules diffuse slightly more quickly. When, as in our experiments, the difference in temperature is only 11° C. the increase is less than 2 per cent.

To test our apparatus and the correctness of our mixtures of sulphuric acid and water we determined the rate of drying of small discs of asbestos paper suspended in the bottle destined for the flea experiments. A disc was placed in one of each of three of the small test tubes and two drops (about ·04 c.c.) of water were allowed to drop on to each from a capillary pipette. The tubes were placed in stoppered weighing bottles, weighed and at once put in the cages suspended in the wide-necked bottle which was immersed in the bath at 32° C. and a current of air with a saturation deficiency of 10 mm. driven through the apparatus at the rate of 100 c.c. per minute. After 10 hours the tubes were removed, placed in their corresponding weighing bottles and again weighed. The results were as follows:

| | *Weight before* | *Weight after* | *Loss by evaporation* |
|---|---|---|---|
| 1 | 19·7214 | 19·7066 | ·0148 |
| 2 | 26·4704 | 26·4554 | ·0150 |
| 3 | 20·6190 | 20·6044 | ·0146 |
| | | Mean | ·0148 |

The same experiment was repeated in a bath at 21° C. with the same air current and the same saturation deficiency obtained in this case by bubbling through 45·57 per cent. $H_2SO_4$.

| | Weight before | Weight after | Loss by evaporation |
|---|---|---|---|
| 1 | 17·4035 | 17·3889 | ·0146 |
| 2 | 17·6377 | 17·6231 | ·0146 |
| 3 | 16·4447 | 16·4303 | ·0144 |
| | | Mean | ·0145 |

A 2 per cent. difference in favour of the higher temperature but hardly outside the experimental error.

## THE LOSS OF WEIGHT OF FLEAS ON DESICCATION.

As fleas are covered with chitin one might conjecture that they would be resistant to drying. Such, however, is far from the case. As will be seen from the following table, fleas from the breeding cage lost half their weight by



https://doi.org/10.1017/S0022172400008500 Published online by Cambridge University Press

evaporation in four days at 32° C. (90° F.) in an atmosphere the saturation deficiency of which was only 10 mm., *i.e.* a relative humidity of 72 per cent. at this temperature. The movement of the air through the bottle was so slow that it may be regarded as nil. By this time 84 per cent. were dead and the remainder died before the loss of water reached 60 per cent. of their own weight. The initial water content of the insects was found to be 80 per cent.

*Rate of Loss of Water of* 50 *Fleas.*

T. 32° C. Saturation deficiency 10 mm.

| Time (hrs.) | Weight 50 fleas | Loss of $H_2O$ | % loss of weight | Survivors |
|---|---|---|---|---|
| 0 | ·0308 | — | — | 50 |
| 2 | ·0288 | ·0020 | 6·5 | 50 |
| 4·5 | ·0284 | ·0024 | 7·8 | 50 |
| 20 | ·0250 | ·0058 | 18·8 | 48 |
| 25 | ·0240 | ·0068 | 22·1 | 43 |
| 46 | ·0206 | ·0102 | 33·1 | 34 |
| 51 | ·0198 | ·0110 | 35·7 | 33 |
| 67 | ·0180 | ·0128 | 41·5 | 20 |
| 100 | ·0148 | ·0160 | 51·9 | 8 |
| 125 | ·0136 | ·0172 | 56·0 | 4 |
| 142 | ·0130 | ·0178 | 57·8 | 0 |
| Dried in desiccator to constant weight | ·0062 | ·0246 | 80·0 | — |

The graphs (Fig. 1) in which the results in terms of the percentage loss of weight of fleas and their survival are plotted as ordinates against time in hours show the relation of mortality to drying.

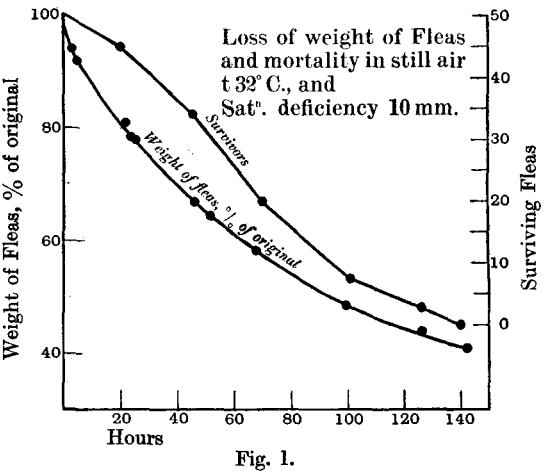


Fig. 1.

THE INFLUENCE OF VARYING SATURATION DEFICIENCY ON THE LONGEVITY OF FLEAS, TEMPERATURE BEING CONSTANT.

A mixed population of fleas, *X. cheopsis*, from the cages were used, 100 for each experiment. In all the experiments the temperature was 32° C. (89·6° F.) and the air current through the bottle 100 c.c. per minute.

The observations were made with saturation deficiencies of 4, 10, 16 and

26 mm. produced by bubbling the air through appropriate mixtures of sulphuric acid and water. At 32° C. these saturation deficiencies correspond to relative humidities of 89, 72, 55 and 27 per cent., *i.e.* from highly saturated to what would be very dry air for natural conditions.

The results are expressed in the series of graphs in Fig. 2 in which the number of surviving fleas is plotted against time in hours. Each graph has the same general characteristic, the descent being steeper as the saturation deficiency increases. The area included between each of the curves and the ordinate and abscissa is proportional to the mean life of the fleas at the particular saturation deficiency.

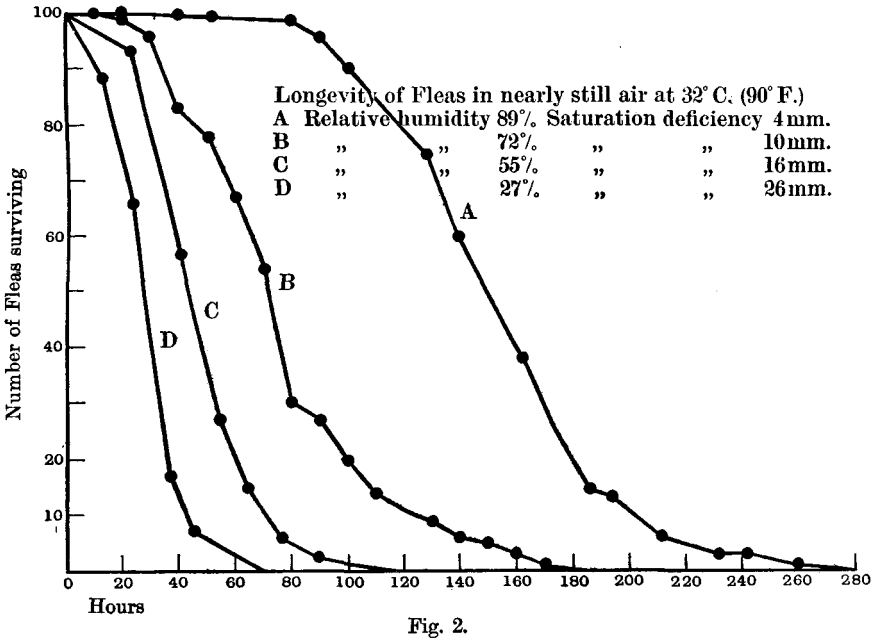


Fig. 2.

The relation of mean life to saturation deficiency is shown in the following table the figures in which are derived by computing these areas after smoothing the curves:

| Saturation deficiency in mm. | Mean life in hours | Mean life × Saturation deficiency |
|---|---|---|
| 4 | 152 | 608 |
| 10 | 68 | 680 |
| 16 | 44 | 704 |
| 26 | 27 | 702 |

By multiplying the saturation deficiency by the mean life a nearly constant number is obtained in the case of the higher saturation deficiencies. This product, however, diminishes considerably at 4 mm. as saturation is approached. Indeed, a departure must occur, for the fleas do not live for ever in saturated air when the saturation deficiency is zero.

We conclude, however, that, apart from this limitation, the mean life of

the insects varies inversely as the saturation deficiency. As the rate of drying also varies inversely as the saturation deficiency, this signifies that, at constant temperature, the mean life of fleas apart from their host is inversely proportional to the rate at which they lose water by evaporation.

### The Influence of Temperature on the Longevity of Fleas when the Saturation Deficiency is kept Constant.

We made but two experiments to determine this, one at 32° C. (90° F.), the other at 21° C. (70° F.). In general arrangement the method was the same as has been described above but the temperature of the bath in the one case was maintained at 21° and in the other at 32° C. In the former the preliminary moistening of the air was omitted, as bubbling it through three bottles containing 45·5 per cent. $H_2SO_4$ in succession was adequate to secure and maintain a vapour pressure of 8·5 mm. in the bottle containing the fleas. This vapour pressure at 21° C. leaves a saturation deficiency of 10 mm. As before, 100 fleas, were used for each experiment. The results are shown in the graphs in Fig. 3

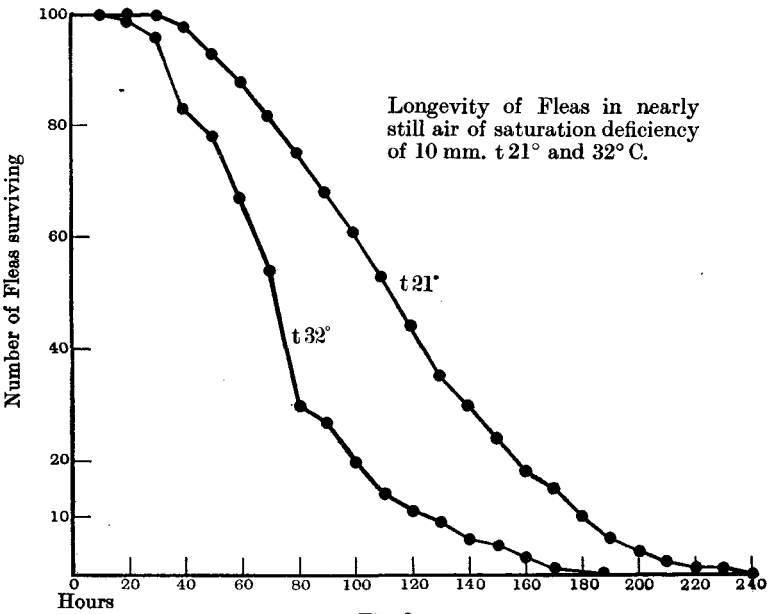


Fig. 3.

which represent the number of fleas alive after various intervals. The mean life of the insects at the two temperatures, derived, as mentioned above, after smoothing these graphs, is 115 hours at 21° C. and 68 hours at 32° C., that is, the fleas lived 1·78 times as long at the lower temperature although they were presumably losing water at the same rate, as the saturation deficiency was the same. This diminished length of insect life at the higher temperature is probably an instance of a general biological law. Those biological activities which have been studied quantitatively in insects are about doubled

by a rise of 10° C.[1] and it has also been shown that a rapid life entails a short one. Loeb and Northrop (1917) found that the life of the imago of the fruit-fly (*Drosophila*) at 30° C. was one-third of that at 20° C.

## Conclusions.

1. The survival of fleas (*X. cheopis*) apart from their host is approximately in inverse proportion to the saturation deficiency of the air, provided the temperature and air movement are constant. In other words, it is proportional to the rate at which they lose water.

2. Under similar conditions but with constant saturation deficiency, their length of life is reduced to between one-half and two-thirds by 10° C. rise in temperature. Compared with the effect of saturation deficiency, that of temperature upon the longevity of fleas is, within the range of climatic conditions over the greater part of India, a smaller one.

3. A variation in saturation deficiency from 5 mm. to 35 mm. such as occurs in the plains of Northern India at different seasons would, accordingly, shorten the average duration of life of wandering rat fleas in the proportion of 15 to 1. As a rise in mean temperature occurs simultaneously with the increase in saturation deficiency and may amount to a difference of 20° C. between January and June this would reduce the length of life of wandering fleas to about one-third. The effect of saturation deficiency and increased temperature will be additive and would go a long way to explain some of the climatological features of the epidemics.

## REFERENCES.

*Annual Report of the Medical Department, Mauritius*, 1899.

Bacot (1914). Bionomics of Fleas. *Journ. of Hyg., Plague Sup.* III. 619.

Bacot and Martin (1914). Observations on the Mechanism of the transmission of Plague by Fleas. *Journ. of Hyg., Plague Sup.* III. 423.

Brooks (1917). The Influence of Saturation deficiency and of Temperature on the Course of Epidemic Plague. *Ibid.* v. 881.

Loeb and Northrop (1917). On the Influence of Food and Temperature upon the Duration of Life. *Journ. of Biol. Chem.* XXXII. 103.

Nicoll (1912). The Length of Life of the Rat Flea apart from its host. *Brit. Med. Journ.* II. 926.

—— (1912). Observations on Flea Breeding in Poona. *Journ. of Hyg., Plague Sup.*, II. 319.

Petrie (1923). *Reports of the Public Health Labs., Cairo.*

—— (1908). Reports on Plague Investigation in India. *Journ. of Hyg.* VIII. 275.

Van Logham and Swellengrebel (1914). Zur Frage der Periodizität der Pest auf Java. *Zeitschr. f. Hygiene u. Infectionskr.* LXXVIII. 141.

[1] A useful collection of data is in Kanitz, *Temperatur und Lebensvorgänge*, Berlin, 1915.