Fleas as Vectors of Plague*

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IT is now well established that fleas are capable of transmitting plague from one host to another. Innumerable species of these parasites have been found on animals throughout the world. Over 80 species have been collected from wild rodents in our western states and new ones are being discovered every year.

As a rule one species of animal seldom acts as the natural host for more than 3 or 4 species of fleas in the same locality, and sometimes for only one. Some varieties of fleas may naturally infest several species of animals, but usually such hosts belong to the same generic group. A few, like the sand flea, appear to utilize almost any animal as their normal host. When different kinds of animals live in close association or come in contact with each other, fleas peculiar to one may be found on others that are not their usual hosts. That fleas may subsist for long periods on blood of animals foreign to them has been demonstrated in the laboratory by keeping many different wild rodent fleas alive for 2 to over 5 months when fed on guinea pigs.

Animals that continually live in the same nesting place, as is usually the case of those dwelling in burrows, harbor more fleas than those that use their nests only for rearing their young. When ground squirrel nests are excavated during the summer, one may see enormous numbers of larvae wiggling about in them, and it is often possible to collect many adult fleas from the nests. Therefore, in determining the extent of the flea infestation of rodents, one must take into consideration the insects that are present in the nesting places as well as those found on the animals.

Climatic conditions play such an active part in determining the prevalence of fleas infesting domestic rodents that in some localities having unfavorable climates there are insufficient vectors to cause plague epizoötics. The potential danger of plague becoming established among wild rodents of any region has little relationship to its climate, being chiefly dependent upon the kind of rodents present and the extent of their population, because wild rodent fleas are as acclimated to their environment as are their wild hosts.

Experimental transmission of plague by fleas—The usual procedure followed in testing the ability of fleas to transmit plague by placing them on an infected rodent, then, after its death, allowing the exposed parasites to infest another animal, provides very little information regarding plague infection of fleas. Positive results obtained from such experiments might be due to infected flea feces rather than to the bites of the insects.

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During the past 2 years experiments have been conducted at the Public Health Service Laboratory in San Francisco in which approximately 1,200 fleas have been tested individually; that is, each flea has been kept in a test tube from the time it was collected until its death. This method provides exact knowledge regarding the time that fleas become plague infected; the period that elapses before they transmit the disease; the length of time the insects survive infection; and, the identity of each flea can be ascertained after its death. Plague infection of living fleas can be determined by inoculation of their feces, and of dead fleas by injecting their bodies into guinea pigs.

Infecting fleas with plague—From the literature on plague one might gain the impression that a flea which has fed at any time on an infected animal might transmit the disease. In reality there is only a short time before death from acute plague that there are sufficient organisms in the blood to infect fleas. The blood of guinea pigs has not been infectious to fleas earlier than 36 hours before death and it is probable that fleas are not infected by the blood of other rodents over a longer time. During this short interval before death the degree of septicemia varies greatly in different guinea pigs. *Pasteurella pestis* may be found in every microscopic field of the blood smears of some acutely sick animals, while in others, blood cultures are required to demonstrate the organisms. As would be expected from the results of blood examinations, the percentage of fleas infected experimentally after feeding on different animals has varied greatly. In most cases only a very small number of fleas have been infected even when the blood examination demonstrated that it contained many organisms, and in no instance has it been possible to infect all fleas fed on one animal. In view of these observations it may be stated that when plague infected animals are killed during the early stages of the disease, or before the development of septicemia, none of the fleas on the animal will have been infected by its blood. Furthermore, even when animals have died of plague, only a small percentage of the fleas on the dead hosts are liable to be plague infected, because only a portion of the fleas that have fed during the septicemic period will be infected, and some fleas do not feed often enough to have ingested blood at this time.

It is doubtful whether fleas ever become infected by feeding on sick animals that recover from acute illness, or that have mild sub-acute infections. In one instance during the experiments at San Francisco a large number of fleas were fed daily for 3 days on a guinea pig that appeared to be so ill each day that it would die in a few hours, and then it began to show signs of improvement which went on to complete recovery. None of the parasites that fed on this animal were infected and blood cultures made during the 3 days of acute illness remained sterile. This guinea pig was inoculated again with plague and recovered a second time.

Multiplication of Pasteurella pestis in fleas—During the act of feeding, blood passes through the esophagus into the proventriculus, and then through a short tubular structure into the stomach proper. The blood is stored during digestion in both the proventriculus and stomach so that ingested bacteria may multiply and form clumps in either organ. More than one mass may be present in the stomach and remain discrete for a long time or coalesce with the formation of one large growth. The rapidity with which the masses grow varies greatly in different fleas. In some only small clumps are present after two or more months, while very rapid growth may occur with extension of the masses into the proventriculus.

In many instances the stomachs are greatly distorted in shape and size by the bacterial growths and have a rather characteristic appearance, being contracted into a more or less tubular form with jagged margins.

Bacterial growths in the proventriculus produce great enlargement of this structure and nearly always extend forward into the esophagus, causing it to be distorted and dilated. Whether or not the masses formed by *P. pestis* develop primarily in the proventriculus or invade it from the stomach, the end results are the same, leading eventually to partial, and then complete obstruction of the esophagus. This blockage has been observed to occur as early as 4 days after plague infection, or it may not develop until several months after ingestion of *P. pestis*. In the case of a number of fleas killed over 3 and 4 months after infection there were no visible masses in the proventriculus and only small bacterial growths were seen in their stomachs.

The dark brown masses formed by the multiplication of *P. pestis* in fleas are not solid clumps of viable organisms but are composed chiefly of colloidal-like material so adhesive that the masses can usually be dissected out intact, and require rough handling to tear them apart. In stained specimens coccobacilli are found in large numbers on the surface of the growths, on the adjacent membranes of the stomach, and in any fluid that may be present.

Transmission of plague by flea bites—From such information as one may obtain from textbooks it would seem that when a host is bitten by a plague infected flea infection will naturally follow the bite. This idea is further from the truth than the belief that all fleas which have fed on an infected animal will be carriers of plague. In San Francisco over 300 fleas have been infected, and they have fed several thousand times and still their bites have not been infectious. There were individual infected fleas that fed from 50 to 100 times on guinea pigs without transmitting plague. Less than 10 per cent of wild rodent fleas acted as vectors in the laboratory, indicating that in nature only a very small percentage of fleas which have fed on infected wild rodents will really infect other animals by their bites.

As long as the bacterial masses do not prevent the passage of ingested blood into the stomach the bites of plague infected fleas are harmless. It is only after development of obstruction to the flow of blood and regurgitation which carries the organisms into the wound occurs that the bites of fleas are infectious. In the course of experiments fleas have transmitted plague as early as 5 days and as late as 147 days after they had ingested *P. pestis*.

Normal fleas of nearly all species seldom insert their probiscides more than once and satisfy their hunger in less than 5 minutes, while the efforts of blocked fleas to feed are often characterized by prolonged exertions to secure blood in one place, or by shifting from one site to another, until they apparently become exhausted. Sometimes a tiny drop of regurgitated blood exudes from the proboscis of an obstructed flea when it is withdrawn from the skin. Many fleas with complete obstruction of the esophagus fail to transmit plague regardless of how prolonged their exertions to feed have been. This may be due to the fact that the blocked fleas are too weak for their efforts to cause regurgitation, or the organisms are not detached from the bacterial growths to be carried into the wounds. After death the obstruction of the esophagus is easily seen with the microscope and frequently fresh red blood is visible in the esophagus in front of the obstructing mass.

Period fleas are infectious—Very few infected fleas survived more than 24

to 48 hours after there were indications that there was an obstruction to the flow of the blood meal to the stomach, regardless of whether or not their attempts to feed were infectious. Of the 45 fleas which transmitted plague in the laboratory only about 20 per cent infected more than one animal, although some of those that failed to cause multiple transmissions attempted to feed after they had infected one guinea pig. Five fleas infected 3 to 5 guinea pigs and one infected 10 animals. This latter flea and one that infected 5 animals transmitted the infection for 5 and 10 days respectively. The infectious life of these 2 fleas was exceptionally long because most blocked fleas live only a short time and few of them are capable of infecting more than one host before they die.

Transmission by male and female fleas—Although many male fleas of different species were used in the laboratory experiments, only 2 of the 45 that transmitted plague were males, which is rather conclusive evidence that female fleas are much better vectors than males.

Plague infection of different species of fleas—During the experiments in San Francisco it has been possible to demonstrate plague infection of 20 different species of fleas, 15 of which were collected from wild rodents, 3 from domestic rats, and 2 miscellaneous fleas. Of the different species found to be plague infected only 11 transmitted the infection to guinea pigs. Domestic rats, prairie dogs, chipmunks, and several varieties of ground squirrels acted as the natural hosts of the fleas which were vectors of plague in the laboratory. Failure to obtain experimental transmission with certain species of fleas does not prove that they are incapable of acting as transmitting agents. In fact the results of laboratory investigation tend to indicate that any flea, regardless of species, that feeds on septicemic blood may become plague infected, and later blockage of the esophagus may occur which would make the flea a potential vector.

Although there is a possibility that all fleas may act as transmitting agents of plague, epidemiological data and laboratory studies clearly demonstrate that the rat fleas, *Xenopsylla cheopis,* are much more active and dangerous vectors of plague than any others tested. A second species of rat fleas, *Nosopsyllus fasciatus,* was found to be as capable of transmitting plague as any of the wild rodent fleas. Some species of fleas seem to be very feeble vectors.

When compared with all other species studied, *Xenopsylla cheopis* are considered the most efficient transmitting agents because they are more readily infected when fed on septicemic blood, and they transmitted the disease to many more guinea pigs. They also tend to become blocked earlier and to remain infectious for a longer time than other fleas. Blocked cheopis are very persistent in their efforts to obtain blood and in many instances they produced 2 to 5 foci of infection on the abdomen of guinea pigs where they had made wounds in their attempts to feed. Some cheopis appear to be capable of infecting guinea pigs every time they insert their probiscides. Multiple foci of infection rarely followed the bites of any fleas except cheopis.

The average length of life of plague infected *Xenopsylla cheopis* is less than 1 month due to the early involvement of their proventriculus by the bacterial growth. Many cheopis did not survive infection 2 weeks, and the longest that any of them lived was about 50 days, while many infected fleas from wild rodents and the rat fleas *Nosopsyllus fasciatus* remained alive from 2 to over 4 months before they became blocked and died.

If different species of fleas do not have the same ability to transmit

plague, and if the infection persists much longer in some species than others, it may be assumed that the character of plague epizoötics will vary according to the kinds of fleas involved in its dissemination. For instance, an epizoötic in a community where *Xenopsylla cheopis* are prevalent should be much more severe and accompanied by a greater incidence of human infection than would be the case in a locality where the spread of the infection depended on one or more of the other species of fleas studied in the laboratory. On the other hand, in regions where cheopis are the only rodent fleas present to maintain an epizoötic, and conditions arise which tend to cause the disease to subside in rodents, so that its continuation depends upon the persistence of the infection in fleas the epizoötic would be more likely to disappear than would be the case if other fleas were present, such as *Nosopsyllus fasciatus,* which may remain infected for a much longer time than cheopis. Wild rodent fleas may remain infected for several months so that it is possible for plague infection to be carried over the hibernating period of wild rodents in fleas.

Plague infection of flea feces—Virulent plague bacilli can be demonstrated in the feces of nearly all plague infected fleas by inoculation into guinea pigs. Some species of fleas do not excrete virulent organisms as constantly as others. The length of time fleas have been infected does not affect the virulence of the bacteria in their feces. In some cases the inoculation of excreta collected at the time fleas have died has produced plague in guinea pigs when injection of the fleas gave negative results.

Since Bacot and Martin demonstrated that fleas transmit plague when feeding, the old idea that transmission followed rubbing infected feces into minute wounds has been more or less discarded. However, it is possible that plague is disseminated among rodents much more frequently through the agency of infectious feces than is generally believed. It is difficult to understand how rodents escape infection in this manner when we consider that one or more infected fleas may live for several months on their hosts and during this time continually deposit large numbers of virulent plague organisms in the fur and on the skin of rodents which will cause infection if rubbed into minute abrasions. It is not necessary for the infectious feces to gain entrance to the hosts' bodies immediately after they have been deposited in order to induce infection because recent experiments conducted at San Francisco have shown that *P. pestis* may retain its virulence as long as 4 weeks in dried flea feces kept at room temperature.

It is unlikely that humans contract bubonic plague through the agency of flea feces because rodent fleas do not remain with human hosts for a very long time and there is slight chance for them to deposit feces on the skin of man. Fleas rarely defecate when feeding and the lesions of rodent fleas seldom cause itching.

Tendency of rodent fleas to attack man—It has been known for many years that domestic rat fleas often bite man, but there is little knowledge regarding the facility with which wild rodent fleas will attack humans. From the fact that 6 different species of sylvan fleas—or all that have been tested in sufficient numbers at the laboratory in San Francisco—have been found to feed on human blood, it may be assumed that many species of wild rodent fleas will bite man. In one instance 18 fleas were collected from a ground squirrel nest shipped to the laboratory and each flea as captured was placed on the arm of one of the workers with the result that 17 of them fed almost as soon as they touched the

skin. It has been possible to keep several kinds of wild rodent fleas alive for a number of days by feeding them on human blood, but others of the same species died of starvation before they would feed on man. Our observations have shown that all rodent fleas have to be starved to a greater extent before they will accept human blood than is required for them to feed on rodents that are not their natural hosts. Many fleas that have refused to bite man were found to feed at once when placed on rats or guinea pigs. From these findings it would appear that starved, blocked, plague infected fleas of wild rodents may attack man when they come in contact with the skin so that there is danger of humans contracting bubonic plague in all regions where wild rodents are infected.

CONCLUSION

Twenty different species of fleas have been infected with plague in the laboratory but only 11 species, 9 of which were collected from wild rodents, transmitted the disease to guinea pigs; only a portion of fleas fed on plague infected guinea pigs a few hours before the animals died were infected, and of those infected only a small percentage transmitted plague to other guinea pigs. Flea bites are not infectious until the masses formed by *P. pestis* cause obstruction of the esophagus. This condition may develop in a few days or not for over 4 months. Few fleas ever infect more than one animal and blocked, infectious fleas generally die within 48 hours of the time there is evidence of obstruction to their stomachs.

Infected fleas are constantly excreting virulent coccobacilli in their feces which may survive for as long as 4 weeks in the dried excreta so that rodents are exposed to infection from the feces as well as the bites of fleas.

There is always a possibility of humans contracting bubonic plague from blocked fleas present on wild rodents in regions where sylvatic plague exists, but these fleas are not nearly so dangerous to man as the domestic rat fleas, *Xenopsylla cheopis*.