PLAGUE AND THE REGULATION OF NUMBERS IN WILD MAMMALS.

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(With 4 Text-figures.)

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1. Introduction.

The object of this paper is to point out certain facts about the regulation of numbers of wild mammals in general, and in rodents in particular, which do not appear to be widely known to medical investigators. It is hoped that some of the ideas brought forward may be of use to students of epidemics in man, and especially of plague epidemics. The great bulk of plague research at the present day is, quite naturally, directed at the problem of the carriage of plague by rats and their fleas, and of other matters directly connected with the disease in man. The present paper deals entirely with plague in wild rodents, *i.e.* it leaves out "domestic" rats and mice. Although less is known about this than about other aspects of the plague question, it will probably be found to be of very great importance in connection with the ultimate origin of plague outbreaks. Plague spreads so slowly, that the origin of any particular epidemic is often unknown, or neglected, owing to the urgency of the immediate problems which are presented.

I am indebted to the following for certain information contained in this paper: Mr H. G. Champion, of the Imperial Forestry Institute, Oxford, for notes on the abundance of hares in Tibet; Mr O. Olstad, of Oslo Museum, Norway, for notes on the abundance of lemmings in Norway; Mr R. H. Coats, of the Dominion Bureau of Statistics, Canada, and the officials of the Hudson's Bay Company, for kindly supplying me with figures showing the abundance of fur-bearing animals in Canada in recent years; Dr Vinogradov, of the Zoological Museum, Academy of Sciences, Leningrad, for data about lemmings in Siberia; Mr W. Rowan, of Univeristy of Alberta, Canada, for information about recent numbers of the varying hare. Finally I wish to thank Dr T. G.

Longstaff and Mr H. Dudley Buxton for help and criticism during the preparation of the paper, and the officials of the Radcliffe Library for their invariable courtesy and assistance.

2. THE OCCURRENCE OF PLAGUE IN WILD MAMMALS.

Before going on to describe the part which epidemics play in regulating the numbers of wild mammals, it will be as well to review shortly those cases in which plague has established itself among wild mammals and particularly wild rodents. There are comparatively few data on this subject, but there are enough to show that epidemics among wild rodents may assume a great practical importance: for instance, an outreak of pneumonic plague, started by marmot infection, caused about 60,000 deaths in Manchuria in 1911.

1. *Marmots in Transbaikalia.* The tarbagan or Mongolian marmot (*Arctomys bobac*), of which an up-to-date account is given by Wu Lien-teh (1923 *b*, etc.), has for some years been well known as a carrier of plague. This rodent is about 15–18 inches in length, weighing about 9–12 lbs., and inhabits treeless steppes in parts of Eastern Europe, extending eastwards over the high steppes in Central Asia, as far as Kamchatka. It is the basis of an extensive industry in Transbaikalia, North-West Manchuria, and Mongolia, where the natives hunt it in order to obtain the skins. The tarbagan is described as being of a fierce disposition, and will turn carnivorous on occasion, although it is usually vegetarian. Clemow (1900) noticed and pointed out a correlation between outbreaks of plague in man and epidemics among tarbagans in 1889 in Transbaikalia. This correlation was observed by workers in later plague outbreaks in those regions (1905–6, and 1910–11), but although it was conclusively proved that the marmot epidemics were caused by the plague bacillus, there was only presumptive evidence that the marmot plague had started before the human one, and was not secondary. In 1923, however, Wu Lien-teh (1924) obtained satisfactory evidence that plague in man may start as a direct infection from natural epidemics in the tarbagan. Infection is probably caused either by the tarbagan flea (*Ceratophyllus silantievi*) biting man, or by the flesh of the animal being eaten, etc. There are two varieties of primary plague: pneumonic and bubonic, and the outbreaks in the marmot area are almost entirely of a pneumonic nature. Since Strong (cited by Liston, 1913) has proved that pneumonic plague bacilli when injected into animals can produce characterictic bubonic plague, it seems clear that the organism is the same in both forms. Liston (1913) points out that pneumonic plague is characteristic of countries with a cold damp climate and bubonic plague of countries with a hot dry climate. He suggests that this difference is caused by drops of moisture in the air, containing plague bacilli surviving longer in a climate of the first type, and thus favouring the spread of the pneumonic plague, while in hot dry countries, where this is impossible, the agents of spread are rats and their fleas. Pneumonic plague in a country like China, once it has established itself, spreads by the breathing of infected air and is independent of rodents. In this connection

it is important to note that it has been proved experimentally that both the tarbagan and a smaller species of marmot (*Spermophilus citellus*) can be infected fatally with plague sprayed in small droplets and breathed in by the animals (Wu and Eberson, 1917).

2. *Other rodents in Transbaikalia.* A good deal of work has been done on other rodents which live in the same localities as the tarbagan, especially by Jettmar (1923). In no case has actual direct evidence of the occurrence of natural plague epidemics among these other rodents been found. But Jettmar gives circumstantial evidence that people become infected with plague from the hamster (*Cricetulus furunculus*) and suggests that these small rodents play some part in the origin of plague outbreaks in man. He gives an account (partly from the work of Dudschenko) of the extraordinary abundance of fleas in the hay-meadows of Transbaikalia in late summer, in the time of mowing (they are referred to as "Flohweide," or "Flea pastures"). The hamster has many fleas in July and none in autumn, and this he attributes to the habit these animals have of putting very strong-smelling *Artemisia* in their burrows, as a food-store for the winter. The strong smell is supposed to drive away the fleas, which take to the pastures, and thus their extraordinary abundance is explained. There is no doubt that certain species of *Artemisia* have an extraordinarily powerful smell, which may have a strong effect on animals. Hooker, while exploring in Sikkim, described how he had a constant headache upon waking in the morning, which he found to be caused by sleeping on a bed of *Artemisia indica.* He noted further that it only produced this effect in damp weather (Hooker, 1854, p. 20). If the smell can have such a marked effect on a human being it may well have equally strong effects on insects. So, although it has not been proved directly that the fleas which haunt the flea-pastures are those of the hamster, there is good reason to think that this is so. Jettmar records that certain families which camped on one of these places died of plague afterwards, in circumstances which excluded the possibility of infection from tarbagans. He also says that local cases of plague occur among children, who are wont to hunt and catch small rodents like hamsters. In another case a hamster, which appeared to be diseased was caught by a cat and killed, and left on a bed in one of the houses. This was followed by an outbreak of pneumonic plague in that house. Jettmar proved that many of the steppe rodents are susceptible to plague, when experimentally injected with it. He found 100 per cent. mortality in the tarbagan and in a smaller species of marmot (*Spermophilus dahuricus*); 50 per cent. in a mouse-hare (*Ochotona dahuricus*); and 25 per cent. in the hamster (*Cricetulus furunculus*).

It is plain that, although more work is required to prove anything for certain, the possibility of rodents smaller than the tarbagan acting as a plague reservoir in these regions cannot be ignored.

3. *Marmots in the Caucasus.* There is another permanent endemic plague-centre in the Caucasus (between the mouths of the Volga and the Ural Rivers). Tchumyé (1909) examined several thousand specimens of rodents and other

animals from there in 1899, but found none infected with plague bacilli. *Spermophilus guttatus* has been found, however, to be very susceptible to the plague bacillus, and according to Manson-Bahr (1921, p. 259) probably spreads it in these regions.

4. *Squirrels, monkeys, and field-mice in India.* Squirrels (*Sciurus palmaeus*) and monkeys have been reported as dying of plague in India (Corthorn, 1899, p. 81). Occasional outbreaks have been noticed on the threshing-floors around plague-infected villages (Anonymous, 1921). It will be remembered that the house mouse is very susceptible to plague.

5. *Gerbils and wild mice in South Africa.* Haydon (1921) has recently proved that plague has established itself among wild rodents in some places on open plains in the Orange Free State, in which country sporadic plague had occurred in man ever since January 1916. He found that the chief species concerned were the gerbil (*Tatera lobengula*), a small rodent slightly larger than the brown rat, and a species of wild mouse (*Rattus coucha*), both of which died of plague in large numbers in 1921. These animals live in burrows and at least one case of human plague was traced to the man sitting over these burrows, while having his lunch.

6. *Musk-rats in Senegal.* The musk-rat (*Crocidura stampflii*) is not a rodent, but an insectivore, which is a common inhabitant of native houses in Senegal, together with rats and mice. Leger and Baury (1922) have shown that it carries plague, but since it is not migratory it does not spread the disease much from house to house. The species which lives in India, *Crocidura caerulea*, has never been found to carry plague bacilli, and appears to be highly immune to the disease.

7. *Wild rodents, etc., in England.* During the years 1906–18, occasional small outbreaks of plague have occurred in man, in a limited area in south-east Suffolk, and these were traced to epidemics in wild rats (for full account see Greenwood, 1924, p. 278). The human deaths occurred at intervals of a few years, viz. in 1906–7, 1909–11, 1918. Since wild rats were observed to be suffering from epidemics in 1906–7 and 1910, it looks as if epidemics occurred periodically among the rodents, and that man was only liable to infection at those times. In 1911 and 1914 it was shown that rats (and in some cases rabbits and ferrets) were carrying plague bacilli, but no mention is made of epidemics.

8. *Ground squirrels in California.* A species of ground squirrel (*Citellus beechyi*), which does not live in contact with man, has been found to act as a reservoir of plague. A flea (*Ceratophyllus acutus*), common both to it and to rats, sometimes transfers the plague to rats, and thence men may become infected by means of the ordinary rat flea (*Xenopsylla cheopis*) (Manson-Bahr, 1921, p. 259).

3. The Regulation of Numbers in Small Mammals.

The numbers of most small mammals do not remain constant; on the contrary, they vary considerably from year to year. This fact is well known to

https://doi.org/10.1017/S0022172400008652 Published online by Cambridge University Press

practical men like farmers, gamekeepers, and foresters, but its importance has not been generally recognised by biologists until recently. For thousands of years it has been known that mice and other small rodents occasionally appear in vast swarms, causing serious damage to land and crops, only to disappear again after a year or two. Well-known cases of this are the migrations of lemmings in Scandinavia, various "mouse-plagues" in Europe and America, and the periodic variations in numbers of Canadian fur-bearing mammals. In a recent paper (Elton, 1924) I have analysed some of the data relating to this subject. It is shown there that there are certain regular laws governing the fluctuations of many small mammals. The main conclusions reached were that there are regular periodic fluctuations and that these are controlled by two types of climatic pulsations, a short one with a period of three to four years, and a longer one with a period of ten to eleven years. Below is given a summary of the evidence on which these conclusions are based. Fuller details on many of the points, together with references to literature will be found in the paper referred to. There is also a good deal of additional matter included here, which was not available when the other paper was written.

1. The periodicity in the number of lemmings in Norway has been worked out in detail. The Norwegian lemming (*Lemmus lemmus*) is a rodent rather smaller than a rat in size, and resembling a guinea-pig in appearance, which inhabits the arctic and alpine parts of Scandinavia, other species being found in other arctic countries. Every three or four years the number of lemmings increases enormously, and in some places the superabundance is so great that migration on a large scale takes place. This superabundance is terminated by an epidemic of bacterial origin, which kills off nearly all the lemmings in the country. The few survivors of the epidemic start increasing again, and after another three or four years again reach a maximum, and so the cycle is repeated. In Canada and Greenland similar fluctuations in lemmings take place, but migration at the maximum is not so marked there. In Norway the records of lemming migrations, which are an index of maxima in numbers, enable us to work out the periodicity in numbers. In Canada there are practically no records of migrations, but the curve showing the number of arctic fox skins taken each year by the Hudson's Bay Company enables us to tell in which year the lemming maxima have occurred, since the arctic fox depends for its food mainly upon lemmings, and the abundance of the latter determines that of the former. When the maxima in Canada and Norway, obtained in this way, are compared, it is found that they have usually occurred in the same years in the two countries (with occasional variations of a year either way, which are, however, made up again at the next maximum). In other words, lemmings are fluctuating in numbers synchronously in Europe and Canada. The four existing records of lemming years in Greenland also coincide with those of Norway. These facts are summed up diagrammatically in Fig. 1. When the last paper was written, no data were available for the years since 1911, except that 1922–23 were lemming years in South Norway. Since then further information has

been obtained. Notes with which Mr O. Olstad has kindly supplied me, show that there was a lemming maximum in parts of South Norway in the years 1918–19, lasting in one case until midsummer of 1920. The official figures for fur production in Canada, issued by the Dominion Bureau of Statistics, show that the number of skins of the arctic fox was at a minimum in 1920, and at a maximum in 1923. This shows that there were lemming maxima in Canada probably in 1918 and certainly in 1922, since the numbers of fox caught in the winter and spring are determined by the number of lemmings in the previous summer.

It will be seen that the lemming years in the two countries and probably in Greenland have coincided in most cases over a period of sixty years, and that the interval between maxima is three or four (rarely two or five) years; but in recent times it has been almost always four years.

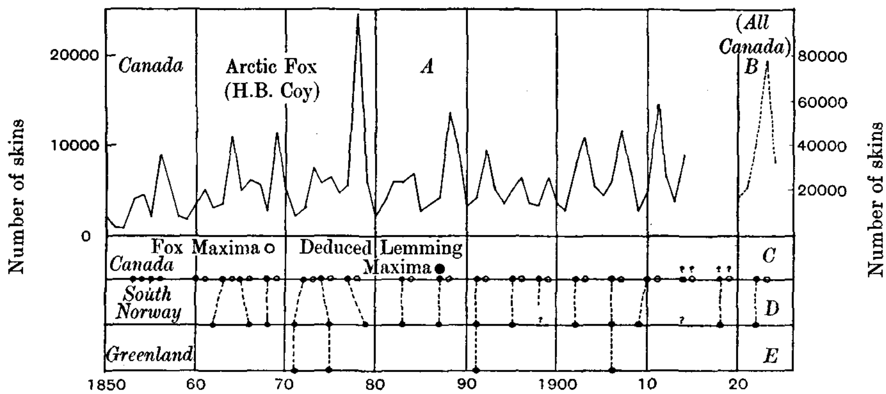

Fig. 1. Periodicity in number of arctic foxes and lemmings. Curve A shows the number of arctic fox skins taken annually by the Hudson's Bay Company in Canada (from Hewitt, 1921). Curve B shows the number of arctic fox skins each year for the whole of Canada from 1920 to 1924 (from the *Dominion Bureau of Statistics Fur Report*, by permission). The vertical scale of B has been reduced to make it comparable with A. Diagram C shows the lemming years in Canada deduced from the arctic fox curves A and B. Diagrams D and E show the lemming years for Norway (data from Collett, 1912, Mr Olstad, and Dr Grieg) and Greenland (data from Winge, 1902; Manniche, 1910; Feilden, 1878). Since a maximum often lasts over two years, dates refer to first onset of migration on a large scale.

Since the number of lemmings fluctuates practically synchronously, not only in different parts of Norway, but in Norway, Greenland, and in Canada, the whole process must be controlled by some widely-acting factor. The only factor of this sort of which we know, and the most obvious, is climate. There must, therefore, be some periodic climatic factor which controls the numbers of lemmings over this wide area.

2. This three or four yearly fluctuation in numbers is not confined to lemmings, although they show it in rather a striking way. On the contrary, there is convincing evidence of a similar short-period fluctuation in field-mice, musk-rats, foxes, etc. In Norway the mouse maxima coincide with those of the lemmings. In Canada there is also a short period in the numbers of mice,

although, as mentioned later on, they also have a strong 10–11-year period in numbers.

It is worth noting that the human plague outbreaks associated with wild rat plagues in England, referred to on p. 141, occurred in 1906–7, 1909–11 and 1918. All three of these periods were lemming maxima in Norway. It is therefore possible that mouse and wild rat maxima coincide in England and Norway.

3. There can be hardly any doubt that it is climate that controls the period of this 3–4-year fluctuation in small rodents[1]. Nothing else will account for the continued coincidence during at least 60 years of lemming maxima in widely separated countries. The question naturally arises: what is this climatic factor? I am at present working on this subject, and the results will be published later on, when completed. Certain things may, however, be pointed out here.

(*a*) One of the most important ecological factors affecting lemming and mouse mortality is cover in winter, whether of plants or snow, which protects them from evaporation, cold, and enemies. In the case of lemmings the snow is the more important of the two things. Since the snowfall varies greatly from year to year in Norway, it is possible that this will turn out to be an important factor controlling the lemming fluctuations. A wet year produces rank vegetation, which affords cover to mice, living in temperate regions. Thus precipitation, whether in the form of rain or snow, affects the protection of mice and lemmings in winter.

(*b*) It is interesting to find that a world-wide cycle of barometric pressure has been shown to exist by the Lockyers (1904). They found that the average annual and winter pressures of India and of the Argentine vary considerably, and have a well-marked period of three to four years, but that the curve for India is the inverse of that for the Argentine, *i.e.* when one is at a maximum the other is at a minimum. Following up this discovery, they found also that the world could be divided into two regions according to the way the pressure varied, one part going more or less with India and the other with South America. Now, North Canada, Greenland and Norway, the areas in which lemming maxima synchronise, fall in one of these regions (that with pressure curve resembling India), while certain places (North Sweden, North Finland, and the Kola Peninsula) which are on the junction of the two pressure regions show abnormalities in the incidence of lemming maxima, and finally the few records of lemming years for Siberia and Novaya Zemlya show that in Siberia, which is in the South American pressure area, the lemming periodicity is

[1] Dr Topley has pointed out to me that it is not necessary to assume a climatic pulsation of three to four years as the controlling factor of these short fluctuations. He suggests that the natural rhythm of increase and epidemics in the rodents would produce the short period and that if these were "brought into line" *occasionally* by climatic factors acting simultaneously in different countries (*e.g.* by the 11-year periodic pulsation mentioned later) they would tend to run automatically in unison in the intervals. This hypothesis is theoretically quite as good as mine, and would perhaps be a simpler explanation if it were not that three or four year climatic cycles actually do exist.

https://doi.org/10.1017/S0022172400008652 Published online by Cambridge University Press

usually reversed, *i.e.* when Norway has a maximum in lemmings Siberia usually has a minimum, and *vice versa*. There is thus a correlation between the lemming phenomena and the pressure variation, in so far as these two regions behave in the same way. (There is not any correlation in detail between the pressure and lemming curves.) This makes it probable that fluctuations in small rodents, with a 3- or 4-year period, are of widespread occurrence over the world.

4. Many small mammals have fluctuations in numbers with a period of the order of 10 to 11 years. The Canadian varying hare (*Lepus americanus*) is the most familiar example, but similar periodicity exists in lynx, fox, skunk, mink, marten, fisher, wolverene, etc., in Canada.

The fur statistics of the Hudson Bay Company show these fluctuations very clearly. At times the varying hares increase to an enormous extent and

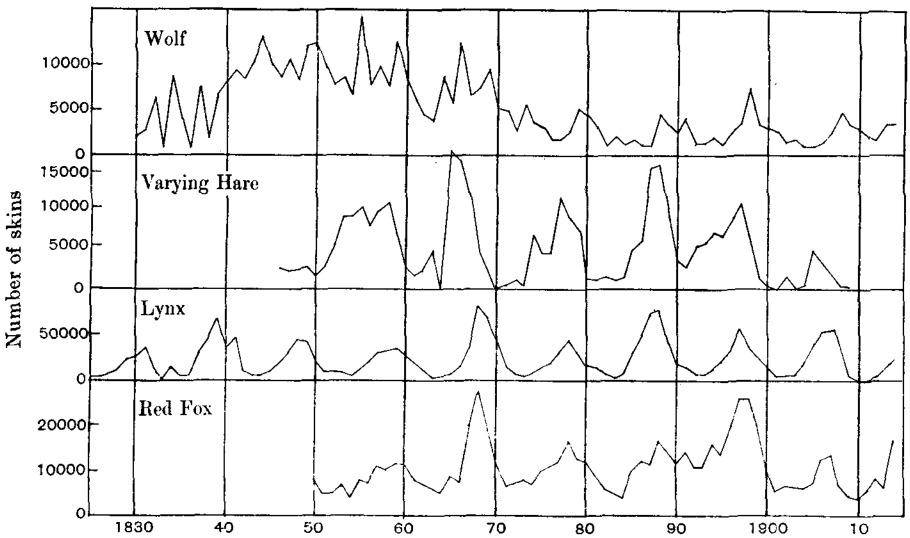

Fig. 2. Fluctuations in the numbers of Canadian mammals (from Hewitt, 1921). The figures for any one year represent wholly or partly the effect of numbers in the summer of the year before. In the case of the lynx there may be a lag of more than one year, on account of various trapping factors.

certain districts become surcharged with them. After this follows an epidemic which kills off most of the hares in the district. Thus the cycle resembles that of the lemmings, but differs in several important respects. First, the years of maximum vary in different localities, although they occur usually within a few years of a definite mean. Thus the curve for the numbers of hares in the whole of Canada, though showing a well-marked maximum, does not enable one to say in exactly which year the maximum occurred in any one small district. In hares there is probably a climatic factor acting in the summer which causes the periodic abundance. In a "good" year, *i.e.* a year of maximum abundance, the fertility of the hares is much increased, there being eight to ten young in a brood instead of the usual five to six, and two to three broods

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in the year, instead of one to two. In a "bad year," *i.e.* after an epidemic, the reproductive capacity is reduced below the normal. It seems probable, therefore, that the cause of this increased reproductive capacity is unusually good climatic conditions in summer, during the breeding season. This reproductive cycle does not however occur in lemmings.

In the paper referred to above, I have attempted to show that the 10–11-year cycle in numbers is mainly controlled by the climatic cycle which is associated with the 11-year sunspot cycle. The number of sunspots is an indication of changes taking place in the sun's radiation, and the latter are believed by many people to be the main cause of an 11-year cycle in world weather, which is however sometimes interfered with by terrestrial factors, such as volcanic eruptions. A full discussion of this question will be found in the other paper. For the present purpose it is sufficient to point out that there is certainly some widely acting 10–11-year climatic factor at work, whatever its ultimate cause, and that fluctuations in the numbers of many animals are correlated with it. Examples of phenomena which are affected by this cycle of climate are: variation in the average temperature of the earth; in the growth-rings of the redwood tree in California, and of pine-trees in Germany; in the levels of lakes (especially clearly shown in Lake Victoria); in the number of tropical cyclones; in the tracks of storms in North America; in atmospheric pressure and rainfall, though these are less marked than the other things, because they are separate factors, while the other phenomena to some extent integrate several climatic factors. To these we may add the synchronisation of fluctuations in the numbers of mammals in Siberia and Canada, pointed out later on p. 155.

5. The fluctuations of mice also have a 10–11-year period, and in some countries, as in England, it becomes more important than the shorter one. Like the hares, they probably have larger and more frequent broods in good years. This can be deduced from the fact that many species have twice as many mammae as there are young in a brood in normal years, the extra mammae being apparently for the periodic good summers. (The varying hare has eight mammae, and normally five to six young, going up to eight to ten in good years.) Mouse "plagues" often occur simultaneously in widely separate countries.

6. The facts given above are only a few selected as examples of what is actually a very widespread phenomenon. This curious method of regulating the numbers, by increasing for some years up to a density necessary for an epidemic, which kills off nearly all the animals, probably occurs among nearly all rodents. Fig. 3 shows how the process is related to the size of the various animals. In an animal community there are herbivorous mammals of various sizes, *e.g.* mice, hares, and deer. The rate of increase of these animals is directly correlated with their size, since a large animal takes longer to grow to maturity than a small one (the period of gestation is longer, and the number of broods therefore smaller). Mice are small and therefore breed fast enough to fit in

with a 3–4-year cycle and also into a 10–11-year cycle, the longer period usually acting by intensifying one of the smaller maxima. Hares breed more slowly and only show a marked 10–11-year cycle. Deer breed so slowly that they show no regular effects of either cycle. This point is well shown if one works out the theoretically possible rates of increase of these animals. A pair of lemmings or mice would increase, if unchecked, to over a hundred thousand in four years, a pair of hares to over ten thousand, and a pair of deer to less than ten.

Carnivores are affected partly by their own size, and partly by that of their food. Fig. 2 shows that the red fox, which preys on mice and hares shows a resultant of the two periods, while the lynx, which eats only hares, has prac

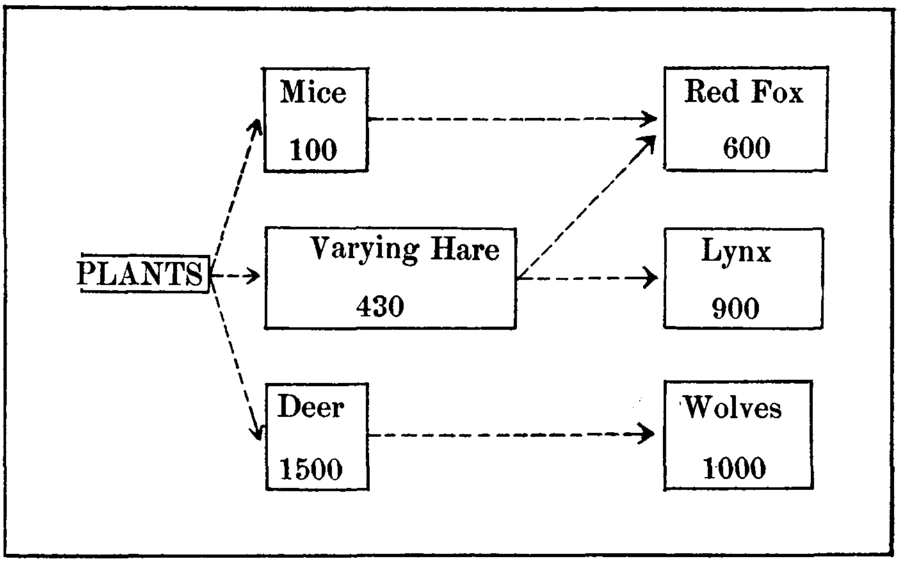

Fig. 3. Diagram of part of an animal community in Canada. The arrows point from the organism eaten to that eating it. The figures are lengths of the animals in millimetres (average for both sexes, tip of nose to base of tail).

tically a smooth 10–11-year period. Wolves show practically no regular short cycle of numbers, since they prey on deer, etc. In recent years, however, Canadian wolves have shown a distinct 10–11-year cycle (see Fig. 2), corresponding to that of the varying hare. This is correlated with the reduction in numbers of large ungulates (*e.g.* bison) which has compelled wolves to adopt a different and smaller food.

Another point, shown by Fig. 3, is that the carnivores are always a good deal larger than their prey (the wolf being virtually much bigger than the deer, since it hunts in packs; the Tibetan wolf, which preys on small antelopes, hunts singly or in pairs, and only occasionally in packs) (Rawling, 1905, p. 316). The result is that the carnivores have a slower rate of increase than their prey. Indeed, the whole point of the carnivore's existence is that it is devouring the extra numbers of herbivores produced by the higher rate of increase of the latter. As long as the rate of reproduction of the prey remains constant, as in normal years, the enemies are able to control the numbers of the former. But if the rate of increase of the herbivore is suddenly accelerated by good climate, *i.e.* if its rate of increase breaks out, so to speak, beyond a certain point, then the carnivore is entirely unable to accelerate at anything like the same pace, owing to its size, and consequently fails to control the numbers of its prey. We find in fact that the numbers of small herbivorous mammals are ultimately controlled by organisms smaller than themselves, *e.g.* bacteria or protozoa. If these sudden increases in animals were only local it would be possible for the enemies to keep them under by migration and local concentration, after the manner of fire-brigades with an unusually big fire. This happens to some extent with lynxes and owls. But when the increase is synchronous over huge areas, such a method of control becomes impracticable. This is the significance of epidemic diseases among rodents. In some cases, however, the carnivore may be an important factor in the life-history of the parasite. Certain tapeworms cause epidemics among rabbits and hares (*e.g.* jack rabbits in California (Nelson, 1909)), and since the bladder-worm stage is passed in the rabbit, it is probable that the adult tapeworm lives in the fox or coyote which eats the rabbit. In this case increase in rabbits accompanied by increase in foxes would speed up the circulation of the parasite, and thus *cause an epidemic. Such a process has been described by Fasten (1922) in* the case of trout and birds. Lake Cooper, Washington, was closed to fishermen for six years, and as a result of this the trout multiplied greatly. All was well for a few years, but an epidemic then occurred among the trout, which was traced to the cysts of a species of tapeworm. Fasten states that the alternative host of the parasite is probably the blue heron, since a similar cycle of hosts was shown by Linton to exist in the white pelican and fish in Yellowstone Park. In Lake Cooper the aquatic birds had increased in numbers with the closing of the lake, and the tapeworm epidemic was probably due to faster circulation of the parasite. If this phenomenon were to occur among rodents, it would be a vital factor in the increase in rabbits in places like Australia and New Zealand, where the rabbit was introduced without its enemy being also brought in.

7. The periodic epidemics which have been described occur in many species of mice, lemmings, hares, rabbits, squirrels, etc. The organism causing the epidemics among short-tailed field-mice is probably bacterial. They have been artificially infected with a bacillus (*B. typhi-murorum*), as a means of checking their numbers, *e.g.* during the Scottish mouse plague in 1891–2, but it does not seem to be very effective (Maxwell, 1893, p. 121). During the Nevada mouse plague of 1907, no trace of any specific bacillus was found, and attempts to infect the mice with mouse typhus failed (Piper, 1908, pp. 304, 306)[1]. Lemmings apparently suffer from a definite bacterial disease at their maxima, the organism

[1] References to mouse-typhus will be found in full in a large paper by Schander and Meyer (1923).

https://doi.org/10.1017/S0022172400008652 Published online by Cambridge University Press

being called *B. pestis-lemmi* (Horne, 1912). Hewitt (1921, p. 219) states that the varying hare epidemic in Canada is bacterial, but hares and rabbits suffer also from tapeworm and nematode epidemics (Nelson, 1909; Collett, 1912). Really, little is known about natural epidemics in rodents, and what knowledge there is is of rather a casual nature, except in the case of plague itself. It may be mentioned that the shrew (*Sorex araneus*) has annual epidemics which appear to kill only the parent generation of the year (Barrett-Hamilton, 1910, p. 107). In Norway, at any rate, shrews also have larger periodic fluctuations in numbers, like those of the lemming (Collett, 1912, p. 9).

Carnivores appear to die from exposure and starvation in winter, when their food has died from epidemics. They do not usually seem to have specific epidemics on the same large scale as the herbivores.

It is worth emphasizing that practically nothing is known about the causative organisms in these rodent epidemics, except in the case of plague, and one or two others. The possibility of rodents acting as reservoirs for other human diseases should therefore not be ignored.

4. FLUCTUATIONS IN THE NUMBERS OF MAMMALS IN EASTERN ASIA.

1. Periodic fluctuations in numbers, the normal mechanism by which small rodents regulate their numbers, have been shown to exist in Europe and North America. The important question from the point of view of plague investigation is whether mammals in Asia fluctuate in the same manner. This question can be answered in the affirmative. The evidence which follows goes to prove that Asiatic rodents, and the carnivores dependent on them, fluctuate in the same manner as the others, some having a short period of three to four years, and others having a longer one of ten to eleven years. Furthermore, the 10–11-year periodic fluctuations are more or less synchronous in Eastern Asia, and in North America, just as the lemmings, with their shorter period, synchronise in Canada, Greenland, and Norway. (The areas in which they synchronise differ in the long and the short periods.)

2. The mammal communities of Asia are of the same type as those of North America, although most of the species are different. We have seen that the two cycles in numbers of Canadian and European mammals may be connected with two world-wide cycles of climate, the 3–4-year pressure cycle and the 11-year cycle in radiation from the sun. We should therefore expect, *a priori*, to find the same fluctuations in mammals in Asia as in the other countries; indeed, they should be more regular since over very large areas the Asiatic mammals have been less affected by civilisation and cultivation than have those of North America, and probably represent a condition of things existing in America before the arrival of white men, and in Europe at the time of Julius Caesar.

3. There is not the same favourable material for analysing the abundance of Asiatic mammals. There are, however, numerous scattered records, which, when pieced together, give us a fairly clear picture of what is happening.

Radde (1862, pp. 141–6), who carried out extraordinarily good field work on mammals in the Amur district and in Transbaikalia, between the years 1855 and 1859, made very full notes on the abundance of squirrels, etc., in different years. This he was able to do because the inhabitants make their living by hunting fur-bearing animals, and therefore keep an anxious eye on the numbers. His observations show that squirrels were very scarce in Transbaikalia during the years 1849–52, and still uncommon in 1855. But about 1856 they began to increase, reaching a maximum in 1857–8, when unusually large numbers were seen, especially during the autumn migrations. There was also an unusually large migration of squirrels in the Bureya Mountains in the *Amur district to the east of Transbaikalia, in 1856. This evidence shows that* the squirrels reached a maximum at about the same time over a very wide area, over a thousand miles in extent. The abundance was followed by a scarcity, which was noticed in Transbaikalia in 1859.

It is interesting to find that there was also a very big squirrel migration at Krasnojarsk in 1847, ten to eleven years before the one in Transbaikalia in 1857–8. Krasnojarsk is about 500 miles west of Lake Baikal. Middendorff (1875, p. 865) recorded figures for the number of skins taken annually by the nomads of the Ulusses Oljokma region (north of Transbaikalia for eleven years 1834–44). These show that squirrels were increasing steadily from 1834 to 1842, when a maximum was reached, and followed by a decline in numbers. The period of abundance extended from 1839–42. Data on the numbers of squirrels in Siberia is scanty, but what there is proves that they fluctuate greatly in numbers from year to year. Nansen (1914, p. 165) notes that there was a great scarcity of squirrels in the Upper Yenisei region in 1913, and remarks that "the great variation in the numbers of these rodents must certainly be due to the ravages of epidemics, as in the case of the lemming." Apparently the maximum was in 1911–12 in that region. Brehm (1897, p. 253) records a great squirrel migration at Tapilsk in the Ural Mountains in 1869.

There is plenty of evidence that many other mammals in Siberia also vary greatly in their abundance. Radde (1862, p. 210) points out that it is impossible to generalise about the local abundance of species (*e.g.* hares, squirrels, etc.) in a given place, unless account is taken of the variation in numbers from year to year. Middendorff (1875, p. 865) remarked that the gradual extinction of certain animals like the sable is masked sometimes by the fact that in certain years there is a temporary revival in numbers. His figures (mentioned above) show that the sable, polecat, and fox vary in a similar sort of way to the squirrel, although the fox also has a marked 3–4-year period. Radde's data also show that the sable varies like the squirrel.

4. The *plague marmot* or *tarbagan* (*Arctomys bobac*) has been studied a great deal, but there is practically no direct evidence as to its numbers in different years, chiefly because it occurs in rather out-of-the-way places. We can, however, get at the facts indirectly by collecting data on the following points:

(*a*) *Epidemics*. The tarbagan is well known to suffer from epidemics of

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pneumonic plague. Ching (1912, p. 29) states that it has an epidemic every autumn, and other workers seem to assume the same thing. There is little doubt however that these epidemics are usually mild, or confined to a few individuals, and that periodically there are much worse epidemics which kill off many of the marmots. In 1911 the tarbagans suffered from epidemics in various parts of Transbaikalia, but for some years after (until 1921) no serious ones were recorded. In fact, Wu Lien-teh was so struck by this fact that he became convinced for a time that tarbagan epidemics were not important in spreading plague to human beings (Wu and Pollitzer, 1923, p. 29). In 1923, however, he was able to prove the direct connection between tarbagan and plague outbreaks. In the marmot and other rodents, just as in human beings, the disease probably appears in the form of mild epidemics between the big ones, killing off only a few individuals. Table I summarises all the data which I have been able to collect about marmot epidemics and other indications of their abundance.

(*b*) *Migration.* When these occur among rodents, they are nearly always an indication of crowding in the population. Radde (1862, p. 161) records one definite case of migration in 1853, in Transbaikalia. According to Anthony (1923) the yellow-bellied marmot of North America (*M. flaviventer*) migrates occasionally. Ching was told by the native hunters of the tarbagan that "the sick animals are often expelled from the holes by the healthy ones, and consequently have to wander aimlessly until they die or are killed on the plains" (Ching, 1912, p. 29).

(*c*) *Number of young and number of mammae.* There is some evidence that certain rodents which fluctuate periodically in numbers (*e.g.* varying hare) have a larger number of mammae than at first sight appears necessary, and that this is correlated with the fact that in years of abundance the number of young in a brood is greater. (This rule does not, however, hold for ungulates.) The European marmot (*Arctomys marmotta*) has ten mammae and usually only two to four young in a brood (Giebel, 1859, p. 628). Similarly, Wu Lien-teh says of the tarbagan (*A. bobac*), which also has ten mammae: "Regarding breeding, there is reason to believe that it is not so prolific as the rabbit—two or three being the average number of young ones born each season" (Wu Lien-teh, 1914, p. 40). It is therefore possible that the tarbagan has larger broods periodically. This fact, if it were established, would be of immense importance, since by examining summer broods it might be possible to predict whether a bad epidemic was going to occur in the autumn, or following year. This is the method actually adopted by the Indians of the Athabasca-Mackenzie region in Canada. They count the number of embryos in the female varying hares in order to forecast how many hares there will be in the following year (Preble, 1908, p. 201).

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Table I. *Abundance of marmots* (Arctomys bobac) *in Eastern Asia.*

1853. *Transbaikalia* (Urunkan—possibly the same as Uriankhai—Valley). Migration of *A. bobac* into the valley, noted as an unusual occurrence. (Radde, 1862, p. 161.)

1876.–1877. *Eastern Tien Shan Mountains* (Yulduz Valley). Marmots abundant. (Prejevalsky, 1879, p. 44, etc.)

1889. *Transbaikalia* (Aksha and Soktui). Epidemic among *A. bobac.* (Clemow, 1900, p. 169.)

1906. *Transbaikalia* (Abagatui). Severe epidemic among *A. bobac*, with high mortality. (Barykin, cited in *Lancet*, 1909, I. p. 1863.)

1907. *Same place.* Only a few *A. bobac* dying of disease. (*Ibid.*)

1911. *Transbaikalia* (between Borsa and Tschintansk). *A. bobac* very abundant. No trace of sick animals. (Wu Lien-teh, 1913, p. 534.)

Transbaikalia (Araboulak and Lake Tshcaborda). Epidemic among *A. bobac.* (Pissemsky, cited by Petrie, 1924, p. 399.)

Transbaikalia (Scharasone, and south of there). Epidemic among *A. bobac.* (Wu Lien-teh, 1914, p. 22.)

Transbaikalia (Borsa). Epidemic among *A. bobac.* (Zabolotny, cited by Petrie, 1924, p. 399.)

North-East Mongolia (Kulun, See). Plenty of burrows of *A. bobac*, but no marmots there. The scarcity attributed to migration, but probably caused also by the epidemic. (Wu Lien-teh, 1913, p. 534.)

Altai Mountains (Dzungaria). Marmots and other rodents almost everywhere in great numbers. (Carruthers, 1913, II. 551.)

cording
marmot
regions during the past ten years, only isolated cases of tarbagan plague have been found." (Wu Lien-teh, 1922 *b*, p. 86.) Later he stated that there was definite evidence of plague epidemics in 1921. (Wu Lien-teh, 1924, p. 329.) In 1919 a Russo-Chinese scientific expedition visited Mongolia and Siberia and found only one tarbagan with complete evidence of plague. (Wu Lien-teh, 1923 *b*, p. 49.)

1923. *Transbaikalia* (Soktui). Epidemic among *A. bobac.* (Wu Lien-teh, 1924, p. 329.)

N.B. The occurrence of human plague has in no case been taken as evidence of marmot plague, although in several instances the disease started in human beings in the year before it was discovered in marmots, owing to the inevitable delay in examining the country after an outbreak was recorded. Thus there were outbreaks in man in 1894 (rather indefinite information from Clemow (1900), stating that the human plague was caught from marmots); in 1905 (Anonymous, 1909); and in 1910 (Ching, 1912).

All these different lines of evidence (summed up in Table I) make it fairly certain that the tarbagan fluctuates in numbers considerably and that periods of abundance and scarcity often coincide over wide areas (as in 1911). The question of the length of the period of fluctuation will be discussed later on.

5. *Hares.* Radde points out (1862, p. 210) that hares vary in numbers from year to year in Transbaikalia, and Nansen mentions the same thing for the Yenisei region (1914, p. 165). There are plenty of scattered records in the literature of travel in Asia, and one could go on indefinitely amassing notes on the subject. I have gone through a large number of such works of travel, and the information obtained from them about the abundance of hares is summed up in Table II.

Table II. *Abundance of hares in Eastern Asia.*

1848. *Western Tibet.* Hares frequent all over the plain of Guge. (Strachey. 1900, p. 248.)
1849. *Eastern Tibet* (Cholamoo Lakes). Many *Lepus oiostilus.* (Hooker, 1854, II. 157.)
1853. *Tibet* (Poogah Lake). *L. oiostilus* common. (Adams, 1867, p. 280.)
1856. *Transbaikalia* (Sassutchiar). Unusual abundance of two species of hares (*L. variabilis* and *tolai*). (Radde, 1862, p. 210.)
1870. *Tibet* (Pangong Lake). Hares plentiful. (Henderson and Hume, 1873, p. 59.)
1876. *East Turkestan* or *Sin Kiang* (Tarim Valley). Hares "tolerably numerous" Altyn Tagh: Hares common. (Prejevalsky, 1879, pp. 66, 84.)
1882. *East Turkestan* or *Sin Kiang* (near Kuldja). Woods full of game, including hares. (Lansdall, 1885, p. 193.)
1889. *N.E. Tibet* (Yohuré). Country alive with game, including hares in large numbers. (Rockhill, 1891, p. 159.)
Central Tibet. Hares abundant or fairly abundant. (Bonvalot, 1891.)
1892. *Eastern Tibet.* Practically no hares seen. "I suppose some animal must destroy them, for the Tibetans neither kill nor eat their flesh." (Rockhill, 1894, p. 311.) Cf. 1889, above, however.
Western Mongolia (between Koko-Shuli and Dungburé). A great many hares. Namchutola, etc.: hares "wonderfully plentiful." (Rockhill, 1894, pp. 201, 203, etc.)
1903. *Western Tibet* (Rudok region). "At certain places in Rudok where low scrub abounded these hares (*Lepus hispidus*) were found in immense numbers; at one spot...I counted 32 in one patch of scrub in the space of ten minutes. They must, however, change their haunts from time to time, as in two places, Pamzal and Niajzu, where they had previously been reported as very numerous, no trace could be found of them." (Rawling, 1905, p. 317.)
1904. *Altai* (near Bysk, and south of it). Hares numerous in several places. (Turner, 1911, pp. 146, 148, 155.)
1908. *North China* (Shansi). Hares abundant. (Sowerby, 1908, p. 9.)
1909–10 Winter. *North China* (West Shansi). Hares plentiful. (*Ibid.* p. 55.)
1912 Spring. *North China* (N. Shansi). Hares abundant. (*Ibid.* p. 105.)
1912–13 Winter. *Lower Yenisei.* "No hares." (Nansen, 1914, p. 165.)
1913. *Lower Yenisei.* Few hares. (*Ibid.*)
Eastern Tibet (Kyekye). "The usual Tibetan animals of the uplands were abundant,...and hares." (Bailey, 1914, p. 355.)
1922. *South Tibet* (Talung). Many hares in one place, by a lake. (Bailey, 1924, p. 291.)
1924. *South-West Tibet* (Upper Sutlej River). Hares extremely abundant. About 15 to 20 to a mile, seen. (Information from Mr H. G. Champion, who visited these regions recently.)

The table does not pretend to be complete, but it does show the fact of fluctuation in numbers, in many parts of Asia, and that the maxima have occurred at about the same time as those of the marmots. The records and dates at which travellers went to the various places have not been selected in any way, and the gaps between records probably often represent the periods of recovery in the numbers of hares after epidemics. The most significant records are those of Radde in 1856 (maximum in Central Transbaikalia); of Rockhill in 1889 (maximum in E. Tibet) and 1892 (minimum in E. Tibet); of Rockhill in 1892 (maximum in W. China); of Rawling in 1903 (maximum and local minimum in W. Tibet); of Nansen in 1913 (minimum after epidemic); of Champion in 1924 (maximum in S.W. Tibet).

The other notes, giving less definite information, are consistent with a general scheme in which moderate abundance for some years is terminated by

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great abundance followed by an epidemic and a period of recovery. The only case which definitely conflicts with this scheme is that in Sin Kiang (East Turkestan) in 1882. It is possible that this is just a local exception due to chance. It is worth pointing out, however, that the world-wide climatic cycle of ten to eleven years does not act in the same way in all districts at the same time. Huntingdon's map (1923, p. 92) shows the manner in which rainfall varies with the sunspot cycle in different parts of the world. Some places vary directly and others inversely with sunspots. The result is a patchwork appearance of the map of the world. Now, the whole of Siberia east of the Yenisei, Mongolia, Tibet, most of China, and parts of India act as a unit, and vary in the same way as the whole of Canada (more rain at sunspot maxima). A region in Sin Kiang (East Turkestan) goes inversely to this. It is therefore to be expected that the fluctuations of animals there will also be reversed, or in places on the borders of the two regions, irregular. This appears to be so.

6. *Sandgrouse.* Pallas's Sandgrouse (*Syrrhaptes paradoxus*) inhabits the sandy steppes of Asia, *e.g.* the Kirghiz Steppes and the Gobi, but at intervals vast flocks leave their normal habitat and migrate into Europe on the west and China on the east. Europe received huge invasions in the years 1863, 1888, 1908, *i.e.* every 22·5 years on the average. There were smaller invasions in between, which show a periodicity of about 11 years. The details of this phenomenon will be found in my other paper. The migration of these birds is certainly due to relative overpopulation, either lack of food, or increased numbers. Unfortunately, data are lacking to show which of these is the cause. The migrations might therefore be due to natural increase, or to good or bad climate. It is significant, however, that they show the same periodicity as the sunspots, and of mammals such as marmots and hares. It is therefore highly probable that cyclical variations of climate are controlling the process. It is worth noting here that the natives of Shansi, in Northern China, are familiar with the variation in the numbers of these birds. Rockhill (1894, p. 9) says: "The people told me they knew long ago the year would be disastrous, for the sandgrouse had been more numerous of late than for many years, and the saying goes...'when the sandgrouse fly by, wives will be for sale.'" This was in connection with a famine which was in existence in those localities at that time (December, 1891). Famines in the East are often associated with droughts and there is strong evidence that both these occur in India at times of sunspot minima. Clemow states that the tarbagan is said to be abundant in years of drought (1900, p. 171).

7. Having shown that squirrels, sable, marmots, and hares all fluctuate in numbers in Eastern Asia, the next thing is to try and determine the period of the fluctuations. Table III gives the years of maxima of Canadian hares, Asiatic hares, marmots and squirrels, arranged in relation to the years of sunspot maxima and minima. Instead of putting the actual dates in the table, they are numbered relative to sunspot minima so that, *e.g.* -1 means the year before and $+1$ the year after the minimum of sunspots.

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Table III. *Animal abundance and the sunspot cycle.*

Sunspot minima	Sunspot maxima	Canada Hare maxima	Asia Hare maxima	Asia Marmot maxima	Siberia Squirrel maxima
	1839	? 0, −1	?	?	0 to +3
1843		−2	?	?	+4
	1848				
1855–6		−2 to +3	1	−2	+2, +3
	1859–60				
1866		−1, 0	?	?	+3
	1870				
1878–9		−1	?	?	?
	1883–4				
1888–9		−2, −1	0, +3	0	?
	1893				
1900–02		−4			?
	1905	0	−2	+1	?
1911–13		+1, +2	0	−1	0
	1917				
1923		+1	+1	0	?

Note. The Canadian hare maximum in 1924 is from the information of Mr W. Rowan.

It will be seen that the animal maxima come much nearer the minima than the maxima of sunspots, and often actually on the minimum, except for the squirrels, and for all animals round about 1905. The squirrels are rather a complicated case to deal with, since they depend to a large extent on pine-cones for food, and the effect of a good summer is only reflected in the crop of cones a year or two later. The lag in squirrels is thus probably due to the delayed effect of climate on their food. Marmots and hares, on the other hand, depend on grass, etc., which is immediately affected by good climate. The exception that has been noted, in 1905, is of the greatest interest since it occurs both in Canadian and in Asiatic animals. It also appears in the sand-grouse invasions of Europe, there being small ones in 1904 and 1906. This exceptional maximum is probably to be attributed to some world-wide climatic disturbance interfering with the sunspot climatic cycle. The nature of this disturbance has been discussed elsewhere (Elton, 1924, p. 138). The main point is that the exception, if it is not merely a coincidence, must have been caused by climate. It is worth pointing out that there may have been another exception in about 1837, which was a sunspot maximum. There are no figures for Canadian hares as early as that, but the curve for lynx and marten enable the hare maximum to be deduced with some certainty. Judging by these, the varying hare had its maximum in about 1837. Now Middendorff's figures for N.E. Siberia show that there was a squirrel maximum in the years 1839–42, which would bring the good year to about 1837, allowing for the lag of two or three years in the case of squirrels. This conclusion is supported by the curve for polecat and sable skins (Middendorff, 1875, p. 865). There is thus evidence that another exception to the usual 10–11-year cycle took place both in Asia and America.

In considering the likely causes of these periodic fluctuations in animals it should be remembered that the existence of a world-wide cycle of climate rests on pretty strong evidence (see p. 146) and effects a variety of phenomena

—tree growth, lake levels, etc. Opinions may differ as to the cause of this cycle, but the fact of its existence remains. Apart from the general likelihood of animals being affected by this climatic cycle, the synchronisation of these fluctuations in widely separated localities, and the tendency for them to follow the sunspot cycle, are strong evidence that such is the case. The hypothesis that those outbreaks of pneumonic plague, which are caused by marmot epidemics, are connected with this cycle of climate is therefore not so unlikely as might be supposed. More facts are of course required before anything can be decided for certain about what is nothing more than a hypothesis which seems to explain the facts available.

8. It was pointed out above that we should expect to find a short-period fluctuation in numbers of small rodents, of the order of three to four years, in Asia, as well as in Europe and America. There is a certain amount of evidence that this is so, although data are very scarce.

(*a*) The notes made by Wrangell and Kyber during their explorations in the arctic parts of N.E. Siberia (Nijnei Kolymsk region) in 1820–4, show that the foxes and mice fluctuate there every three years. "The natives have always remarked that stone-foxes are abundant every three years and they assured me for the last two years that there would be a great number of young foxes this summer (1822)" (Wrangell, 1844, p. 280). This forecast was confirmed by Wrangell, and his general notes show that the cycle in number of foxes depends on a similar cycle in the number of mice (lemmings are probably included by him under the general term "mice").

(*b*) Middendorff (1875, p. 865) gives statistics for eleven years of the number of foxes and ermine caught by the nomads of the Ulusses Oljokma region, in N.E. Siberia (a good deal south of the area visited by Wrangell). These are shown in the form of curves in Fig. 4. Both the fox and the ermine were evidently fluctuating together, and there is a period of three to four years. This fox is probably influenced by a longer period in the abundance of larger rodents as well as by mice, like the Canadian fox.

(*c*) Allen (1903) notes with regard to the lemmings of N.E. Siberia, "their comparative scarcity and abundance in different years," but gives no information about the period.

(*d*) Radde states (1862, p. 204) (on the information of the native inhabitants) that a certain vole, *Phaiomys* (*Hypudaeus*) *brandti*, which inhabits the Gobi to the south-east of Transbaikalia, migrates occasionally in swarms like the lemming, and invades the Russian territory to the north of its usual range. There are certain species of lemming, which occur in these regions, and which would probably be very good indicators of climatic fluctuations, but unfortunately, as Dr Vinogradov informs me, there is no information as to their fluctuations or migrations. (*Myopus middendorffi* lives on the mountains round Lake Baikal, and *Lemmus amurensis* in the Amur province, near Pikan on the Zeya River.)

(*e*) Hooker, when exploring the frontier of Sikkim and Tibet, noted that a species of rodent (*Lagopus tibetanus*) "sometimes migrates in swarms (like the Lapland 'lemming') from Tibet as far as Tungu" (Hooker, 1854, p. 83).

(*f*) Radde (1862, p. 231) observed a large migration of *Lagomys ochotona* in a valley in the eastern part of the Kablunoi mountains in Transbaikalia in 1851. This was not at the same time as the hare maximum, and suggests a short period like that of mice.

This evidence, although meagre, shows that short-period fluctuations do occur among small animals like mice and mouse-hares, in Asia. In the first two instances the period is one of three or four years, and although these

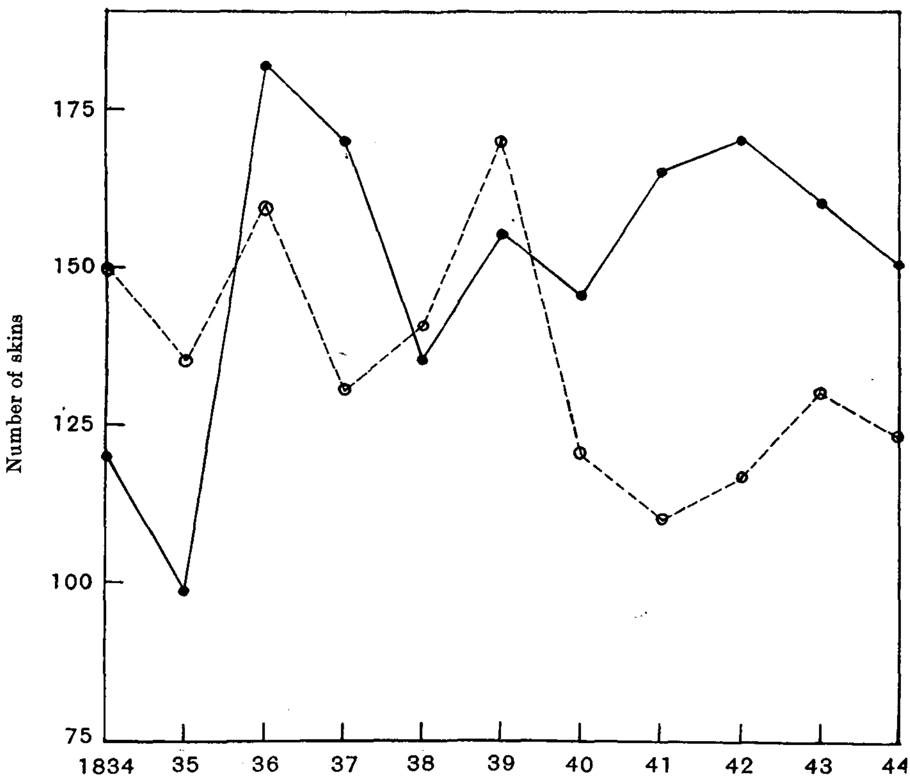

Fig. 4. Periodicity in the numbers of foxes and ermine caught by the hunting nomads of the Ulusses Oljokma region in N.E. Siberia (from Middendorff, 1875, p. 865). Broken line, fox; unbroken line, ermine.

areas are north of the actual plague-marmot area it seems very likely that similar fluctuations are occurring among small rodents there also.

9. Practically nothing is known about the fluctuations of animals in the tropical regions of the world. A knowledge of this subject might be of great importance in plague research. There is only one point on which we have information. I am indebted to Mr H. G. Champion for pointing out to me the existence of a phenomenon which has a great effect upon the numbers of rodents in tropical countries like India. This phenomenon is the periodic flower-

ing and seeding of bamboos. Bamboos are practically confined to the tropics and sub-tropics, at any rate in latitude, although they ascend in some cases high up on to mountains in the tropics. Some species flower every year, but others at much longer intervals, and when they do so often flower gregariously over wide areas in the same year. (An account of this phenomenon will be found in Troupe, 1921, p. 982, from which source the information given here is derived.) For instance, *Dendrocalamus strictus* "commonly flowers sporadically, in isolated clumps or in small groups almost every year. It also flowers gregariously over large tracts at long intervals, gregarious flowering usually taking some years to complete, and often progressing in a definite direction in successive years" (p. 1006). In Garwhal this species has a period of 36–40 years, with practically no flowers in the intervals. Similar periodic flowering occurs among other species, but the periods are different. The whole question of the cause of this is discussed by Troupe; the conclusion seems to be that the periodicity is partly due to internal factors in the plant, and partly to climatic variations. The enormous seed production resulting from one of these gregarious flowerings causes a great increase in small rodents, which benefit by the unusual supply of food. Troupe says: "In Burma it has been noticed that in years of gregarious seeding of bamboos rats multiply freely, and when the seeding is over these pests commit great havoc among the neighbouring agricultural crops" (p. 983). Since different species of bamboos have different periodicities, the effect on rodents must be very irregular. For this reason it is probable that fluctuations in numbers of small rodents in tropical and to a less extent in sub-tropical regions are less regular or at any rate obey different laws to those living in temperate and arctic regions.

It is therefore fortunate that nearly all the endemic plague centres in the tropics are situated on mountains, and have a temperate climate. The regions which have been shown to have endemic plague are Transbaikalia; Yunnan in China; Garwhal and Kumaon in India; Assyr in Arabia; Kurdistan hills above Bagdad; certain mountainous regions in East Africa; and one or two places at sea level such as Benghazi in the Mediterranean (Simpson, 1905, p. 177). Most of these places are situated at height of 5000–6000 feet above the sea, and have snow in winter. It is therefore to be expected that small rodents are fluctuating in some fairly regular manner, and if they are proved in the future to carry plague, it may be possible to predict the epidemics.

5. The Relation of Rodent Fluctuations to Plague Investigation.

An attempt has been made in the preceding sections to describe the general way in which the numbers of rodents are regulated and the part which epidemics play in this process. The most important conclusion which can be drawn is that the epidemics have a definite periodicity in many cases, *i.e.* instead of being irregular and unpredictable phenomena, they obey regular laws, and there is therefore the possibility of forecasting their occurrence. Evidence has been given which points to the conclusion that Asiatic mammals fluctuate in the same way and with the same periods as the mammals of North America and Europe, owing to the fact that the fluctuations are under the control of world-wide cycles of climate. It is useless to enter here deeply into the possible practical applications of these facts to plague control, since that is the business of experts on the spot. There are, however, one or two points which are perhaps worth noting.

1. The fact that diseases appear in rodents in epidemic form only at certain intervals of years is of importance from a practical point of view. Much work has been done in the way of bacteriological examination of rodents for the presence of plague, which has given negative results. From these results it has often been assumed that these particular rodents were of no importance as reservoirs of plague. But the rodents have periodic epidemics, and unless they are examined in the right month of the right year plague may not be found in them, or at any rate it may be in a suppressed or chronic form. This has been recognised by Wu Lien-teh, who says, "our evidence shows that sub-acute or chronic plague may exist among tarbagans in Mongolia and Siberia, and thus form a connecting link in the epidemiology of plague in those regions" (Wu Lien-teh, 1922 *a*, p. 98).

Investigation is usually carried out just after a plague outbreak, and as Wu remarks, "an epizootic among *Arctomys bobac* in the Siberian wastes may well be over before a scientific expedition reaches the spot" (Wu Lien-teh, 1922 *a*, p. 86). If it were possible to foretell the years in which epidemics will occur among rodents in a particular place, then it would be possible to obtain conclusive evidence as to whether they were acting as a plague reservoir or not. Unless they are examined at the time of maximum numbers negative bacteriological evidence is inconclusive.

2. The most important plague outbreaks in the marmot-hunting area of Eastern Asia, in recent times, seem to have been in 1888–89, 1905–6, 1910–11, 1917–18, and 1920–23 (for details see Wu Lien-teh, 1922 *b*), mild and local outbreaks, some of which are traceable to marmots, having occurred in the intervening years. All these, except that in 1917–18, seem to have occurred at maxima in numbers of the marmot (*A. bobac*). In 1917–18 htere was definitely no severe marmot epidemic. Jettmar (1923) has brought forward considerable evidence to show that the hamster (*Cricetulus furunculus*) may have been the source of infection then. This would fit in with the idea that small rodents like hamsters and mice and mouse-hares (*Ochotona*, etc.) are fluctuating in numbers every three or four years in these regions, with epidemics at each maximum. (There is little contact between men and hamsters, while there is very intimate contact between men and the tarbagan. It is therefore much more likely that a plague outbreak in man will result from tarbagan epidemics than from hamster or mouse epidemics, even though the latter occur three times as often as the former.)

3. It must also be remembered that the tarbagan will eat small rodents such as hamsters and mouse-hares (Jettmar, 1923, p. 327). This introduces

the possibility of tarbagans becoming infected by eating diseased small rodents. It is well known that hares and rabbits in times of overabundance often over-eat their food supply (grass, etc.) and do much damage by barking trees. It is therefore possible that the tarbagan, which lives on vast treeless plains, becomes carnivorous in times of overpopulation. Burrowing rodents like marmots and rabbits can only eat for a limited distance round their holes on account of the danger from enemies, which increases the chance of food supply becoming exhausted. Since mice, etc., would also be on the increase at times of marmot maxima it would be hard to say whether the plague bacilli which have been proved to exist in the latter during epidemics are really indigenous or derived from mice or hamsters. Clemow says (1900, p. 171) that *hares and reindeer* eat the flesh of dead tarbagans, although they do not get the disease afterwards. This would be accounted for in the same way, by the fact that hares and marmots reach their maxima together, and that the general lack of food would affect all herbivorous animals, and cause them to adopt carnivorous habits temporarily.

4. It has been mentioned earlier (on p. 151) that if the number of young marmots varies according to good or bad years, it might be possible to foretell their maxima and corresponding epidemics by examining the number of embryos in the females.

5. With a reservoir in wild rodents there is always the possibility of man becoming infected *via* the "domestic" rat as in the case of ground squirrels in California. There is little doubt that investigation along the lines suggested in this paper would also throw light on the epidemiology of "domestic" rats and mice.

6. If the fluctuations in numbers of tarbagans are correlated with the sunspot cycle, we should expect a period of maximum numbers of marmots to occur between the years 1931–34, since the sunspot minimum should occur in about 1934. There will therefore probably be marmot epidemics in those years. There is also the chance that epidemics among smaller rodents may take place in the intervening years.

6. Summary.

1. A short account is given of the occurrence of plague epidemics in wild mammals other than "domestic" rats and mice. Enough is now known to show that such epidemics are often of great practical importance.

2. The method by which most rodents regulate their numbers is as follows: increase in numbers over several years up to a point at which an epidemic of some sort occurs, which kills off a large proportion of the population. Increase then takes place again, and is followed by another epidemic, and so on indefinitely.

3. These periodic fluctuations are probably controlled by widespread climatic fluctuations, the best evidence for this being that in certain cases the former run synchronously in widely separated countries.

4. There appears to be a dominant short period in fluctuation of three to four years, and a larger movement of period ten to eleven years, both in North America and Europe. The fact that the 11-year sunspot cycle roughly corresponds with the larger movement is significant.

5. The data available from Eastern Asia suggest that there too, small mammals fluctuate periodically in numbers, and with similar periods to those of North America and Europe. There is also some evidence that the maxima of the 10–11-year fluctuations coincide in Eastern Asia and in North America, just as those of the 3–4-year period coincide in Northern Canada, Greenland and Norway.

6. Evidence is given that the plague marmot (*Arctomys bobac*), and other rodents carrying plague, are liable to these fluctuations. If this proves to be true, it may be possible, when fuller data are available, to forecast with some accuracy the years of epidemics among these animals, and if this can be done we shall have some means of gauging the likelihood of the occurrence of plague outbreaks in the human population of those regions.

7. The available data are admittedly fragmentary, but it is probable that between the years 1931 and 1934 epidemics among *A. bobac* in Transbaikalia and Mongolia will be severe, and that these events will lead to an increase of plague mortality in man.

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https://doi.org/10.1017/S0022172400008652 Published online by Cambridge University Press

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(*MS. received for publication* 22. v. 1925.—Ed.)

https://doi.org/10.1017/S0022172400008652 Published online by Cambridge University Press