# PERIODIC FLUCTUATIONS IN THE NUMBERS OF ANIMALS: THEIR CAUSES AND EFFECTS

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CONTENTS



## 1. Introduction.

This paper has involved the study of facts from many subjects both inside and outside the domain of biology, and I am much indebted to the following gentlemen, who have generously helped me in various ways: Mr G. M. B. Dobson for much valuable advice on meteorology and on methods of analysing curves; Mr D. Brunt for allowing me to consult his unpublished work on periodicities in climate; Professor H. H. Turner for advice on astrophysical questions; Dr T. G. Longstaff for notes on a mouse plague in England; Dr S. Ekman for a list of Swedish lemming years; Dr J. Grieg for notes on a lemming year in Norway; Mr P. Uvarov for help with literature on locusts. I wish to thank all these gentlemen, and also in particular Mr J. S. Huxley who has given me much invaluable advice and help during the preparation of the paper.

## 2. Climatic Cycles.

It will be shown in the body of this paper that the periodic fluctuations in the numbers of certain animals there dealt with, must be due to climatic variations. This conclusion follows from the biological evidence alone. Therefore, in order that the facts may be appreciated in their proper bearing, a short summary is given below of what is known on the subject of short-period pulsations of climate, apart from those deduced from animals. (Full treatment is given in the works of Brooks, 1922; Huntington, 1914, 1922, 1923; Humphreys, 1920; Shaw, 1923; and others.)

It is only within the last few decades that we have begun to reach some understanding on the subject of variations or pulsations of climate. Although there is still a great deal of controversy over many questions, on certain points agreement has been reached. Firstly, climate never remains constant; there are the daily and monthly variations we call weather, and there are recurrent seasonal changes; there are variations from year to year and over several years, and finally there are big climatic pulsations such as ice-ages. There is still much disagreement as to the causes of the larger pulsations, but for the present purpose it is only necessary to discuss the minor pulsations of climate of the order of two to twenty years, since it is the effects of these which are so clearly shown by animals and plants. For some time it was thought that these climatic pulsations were simply the chance result of an enormous number of interacting factors, and therefore impossible to analyse. But recent work has shown that there are certain pulsations of climate going on, which are definitely periodic. Much, however, still remains obscure, and the following account owing to its brevity will necessarily give a rather more clear-cut picture of climatic cycles than is really justifiable.

The ultimate source of nearly all the income of energy which the earth receives is the sun. From it we get a continual stream of radiant energy, part of which is intercepted and circulates in the form of our weather and climatic movements, and through animals and plants, before passing off again into space. Plants actually utilise about 2 per cent. of the sunlight that reaches the surface of the earth.

Now it is clear that variations in climate might be caused either by changes in the sun, or by terrestrial events, or by some outside agency besides the sun. The sun varies about 5 per cent. in its output of energy, and this variation has now been definitely proved to affect the earth's climate. The number of sunspots has been observed regularly for over a hundred and fifty years, and these have a well-marked period whose average is 11.2 years, but which actually varies from nine to thirteen years in length. Also, although the minima all approximate to zero, the maxima vary in size, so that there is a well-marked major sunspot periodicity shown by the line joining the maxima of the 11-year periods (fig. 6).

Increase in the number of sunspots is accompanied by increased output of energy from the sun. The evidence for the influence of the sunspot periodicity on the earth's climate may be summarised as follows, and unless otherwise indicated is given in full in the works of the writers mentioned above.

(1) The average annual temperature of the whole earth appears to be, with certain exceptions dealt with later, lower at sunspot maxima, and higher at minima (see fig. 1). At the same time, the number of years for which suitable records exist is not large enough to make this correlation completely convincing. This paradox of a cool earth when there is a hot sun is possibly to be explained by the action of increased radiation of very short wave-length upon the upper atmosphere, rendering it less penetrable to the longer rays (light, infra-red).

(2) The pressures and rainfall of various parts of the world vary in relation to the 11-year sunspot periodicity. The careful work of Walker (1923), who uses the method of correlation coefficients, has proved this clearly. But whereas some regions have more rain at sunspot maxima, others have more at minima, so that we can divide the world into regions according to which way their climate varies.

The effect of the solar variation is probably in the nature of an interference with the normal balance of the atmosphere causing increased or decreased oscillation on a large scale.

(3) Kullmer has shown that the tracks of storms in North America shift about periodically, and that so far as the short series of observations goes, this shift is correlated with the sunspot period. This really means a periodic slight shift of the great climatic zones, and would be a fact of great importance, even if it were shown not to be caused by the solar variation.

(4) Huntington and Douglass have shown that the redwood tree (Sequoia) bears a very clear record of past climate

in its annual rings, and they have been able to carry this record back three or four thousand years. The trees respond to changes in outer conditions of climate by varying the amount of growth of the wood, and if a large number of trees are measured and the rings of individual years compared, very accurate curves can be constructed. Here again there is a well-marked 11-year period, coinciding with that of the sunspots. There are also longer periods. Similarly an 11-year is shown in certain trees from Germany. (This has been attributed to periodic thinning of the forest, but the shape and period of the curve do not support this view.)

(5) Changes in the level of Lake Victoria (Brooks, 1923) and some other lakes are correlated in a very marked way with the sunspot period (*e.g.* a correlation coefficient of +0.87 between Lake Victoria level and sunspots). Here the level is the resultant of rainfall and evaporation, and there is thus an approach to the degree of integration of climatic factors which a living organism is capable of attaining. These are the main lines of evidence showing the importance of solar variation in the earth's climate. It has recently been shown (Hale, 1924) that the sunspots change their magnetic polarity every eleven years, so that there is apparently a 22-year period going on as well.

The amount of variation in temperature on the earth between sunspot maxima and minima is about 0.6° C. in the tropics, and less as one goes further away from the equator, and this is quite enough to be important. It represents from 1/10 to 1/20 of an ice-age, so to speak. A change of 0.5° C. will shift the isothermal line about eighty miles horizontally (Humphreys, 1920), and this is obviously enough to have great effects on animals and plants. It is important to note that a variation in the meteorological observations which may appear quite small, may have enormous effects on living organisms.

The only other factor outside the earth which has been suggested as a cause of fluctuations in climate of the short-period type in is the tidal effect of the moon. The effect on the atmosphere has been shown to be negligible; but Pettersson (1912) has proved clearly that the movements of the herring in the Skagerak and Kattegat are determined by periodic movements of the lower layers of the sea, which in turn are caused by the moon. This short period is one of 18.6 years. He therefore suggests that these hydrographical changes affect the climate of those regions.

Now with regard to terrestrial causes, the only big factor which acts at short intervals and is known to affect climate,

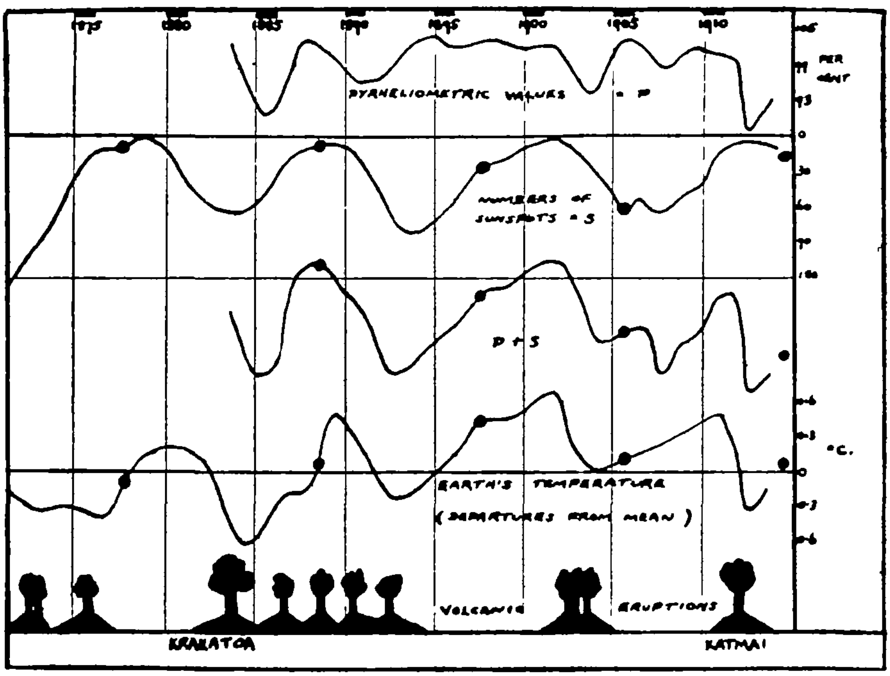


FIG. 1.—Relation between sunspots, volcanic eruptions, earth's average temperature (surface); and maxima in the numbers of the Canadian rabbit (varying hare). (Former from Humphreys, 1920; latter from Hewitt, 1921, see fig. 5). Curve A: Pyrheliometer measurements showing amount of sunlight cut off by volcanic dust. Curve B: Sunspot curve (inverted). Curve C: A and B combined. Curve D: Earth's temperature. (The black dots are rabbit maxima; see p. 135.)

is the eruption of volcanoes. This is, of course, irregular in occurrence. If an eruption is of the kind that sends out quantities of dust, part of the sun's radiation may be prevented from reaching the earth's surface, and a general cooling may result. Such a case of cooling is well seen in the results of the eruption of Katmai in 1912 (fig. 1). If the sunspot curve be combined with the curve (obtained by means of the pyrheliometer) representing the radiation cut off by the volcanic dust, the result resembles that of the earth's temperature much more closely than the sunspot curve alone. Thus the effects of other factors may always be upset temporarily by volcanic eruptions; but the effects of the latter do not last for more than a year or two, and are sometimes confined to one hemisphere only.

It is highly probable that there are other terrestrial factors, hitherto undiscovered, which are influencing our climate. In any case the effects of even a few factors, such as changes in the sun and volcanic eruptions, become very complicated and involved. It has to be remembered that while some of the effects of solar variation might be felt at once, in the case of others there may be a considerable lag. Thus it has been shown (Wiese, 1922) that a cold year in the north of Siberia causes quantities of ice to appear round Spitsbergen about four and a half years later, owing to the time taken for the ice to drift that distance.

There are cycles of climate which cannot be accounted for in any simple way by known causes, *e.g.* the well-known Brückner cycle of about thirty-five years, clearly shown in rainfall and in the changes in level of the Caspian Sea. Separate meteorological factors for any one place show considerable and usually rather irregular variations. Mr D. Brunt has generously allowed me to consult his unpublished work on periodicities in pressure, rainfall, and temperature for various places in Europe (obtained by careful harmonic analysis). These show that the variations from year to year can be analysed into a good many periods whose length varies from 1½ to 35 years. Among these is one of 3½ years which occurs in the temperatures of six stations in Europe. It is not, however, very marked, but is of interest in connection with the period in lemming numbers described later, which is of the same length.

Chree (1924) has recently shown that the meteorological data for Kew show no marked correlation with the 11-year sunspot cycle, and this is also true ~~of Mr~~ Brunt's results, except in the case of Edinburgh. It is the writer's opinion that these facts do not disprove the idea that the solar variation may have important effects on animals and plants through climatic changes, since living organisms integrate the separate meteorological factors. That is to say, the original energy from the sun is split up into numerous separate manifestations (those studied by the meteorologist) which are reintegrated by the organism. A good climate, like a good dinner, is more than the mere sum of its separate parts. It is therefore important to note that the best evidence for the existence of 11-year cycles of climate is from lake-levels, which to some extent integrate climatic factors like an organism, from tree-rings, and as will be shown, from animals. This is what we should expect.

### 3. Periodic Fluctuations in Animal Numbers.

**Lemmings.**—The lemmings are a group of rodents, resembling in appearance small guinea-pigs, which live in arctic and sub-arctic countries, where they occupy the ecological niche of the mice and rabbits of lower latitudes. Evidence is given below that the numbers of lemmings fluctuate periodically all over the arctic regions.

1. *Southern Norway.*—The Norwegian Lemming (*Lemmus lemmus*) inhabits the arctic regions of Norway down to sea-level, and occurs further south in the mountains. It follows the zone of arctic-alpine tundra, above the tree limit, which in the mountains of South Norway is about 3000 to 4000 feet above sea-level. The data about the lemming are taken from Collett (1911).

For many years the lemmings have periodically forced themselves upon public attention in Southern Norway by migrating down in swarms into the lowland in autumn, and in many cases marching with great speed and determination into the sea, in attempting to swim across which they perish. The details of the fate of the migrants do not concern us here and are fully described by Collett. The main point is that all these lemmings die, and none return to the mountains, the chief cause of death being an epidemic bacterial disease. It seems pretty certain that the immediate cause of the migration is overpopulation in the usual habitat. Lemming pairs usually have their own territory, nearly all the migrants are young animals of that year, and while large numbers are concerned in migrating, each individual still remains solitary and pursues its own independent course. These facts, taken with the stupendous numbers of migrants, and the fact that a certain number of lemmings stay behind and do not migrate, show that the phenomenon is analogous to infanticide among human beings as a method of preventing overpopulation. As a matter of fact the epidemic also attacks the stay-at-home animals, and thus the population is still further reduced. The lemming-years are such conspicuous phenomena that it is safe to assume that all which have occurred (since about 1860) have been recorded. Lemming-years in Norway have the status of great floods or terrible winters.

It should be remembered that lemming migration is only an indicator of overpopulation which passes a certain point, and therefore lemmings might have a small maximum which did not lead to migration. A study of the lemming-years of South Norway leads to the following results :—

(*a*) Lemming overproduction occurs periodically every few years and culminates in an autumn migration. It is usually found either that some of the migrants of that year survive the first winter and carry on the invasion of the lowland in the next summer, or else overproduction in one district is followed in the next year by overproduction in a neighbouring one; so a lemming maximum may cover one or two years. For this reason, owing to the difficulty of knowing when the maximum has ended, in the following treatment, the first year of onset of migration is taken as the maximum, except in 1890 and 1894, when the migration was very small compared to that of the next year.

(*b*) The area of great over-increase varies in size and position, but often includes several distinct, and for lemmings isolated, mountain blocks.

(*c*) With one exception, a lemming maximum has occurred every three or four years (occasionally two or five). See diagram C, fig. 2.

(*d*) The exception noted above is the year 1898. It is probable, in view of the evidence to follow (p. 132), that there was a maximum of lemmings in the mountains, but not sufficient to cause a migration, especially as there was one in North Finland in 1897.

(*e*) If we assume a maximum in 1898, the mean period between maxima is 3.6 years (1862-1909).

I have not been able to obtain full information of lemming-years since 1910, but Dr Grieg informs me that there was one in the Hardanger region in 1922-1923. It is highly probable that records will be found for 1914 and 1918.

The Wood Lemming (*Lemmus* (*Myopus*) *schisticolor*) which lives lower down on the mountains than its ally, is also subject to "good years" followed by migration. So far as the data go, over-increase is found to take place in the same years as the common lemming (1883, 1888, 1891-92, 1894-95, 1902, 1906).

2. *Southern Sweden.*—The lemming-years in Sweden have not been recorded so regularly as those in Norway, possibly because the cultivated land is not so often invaded. The records of some of the years are probably based on abundance and not on migration, so that they do not afford such an accurate index of the actual maximum as those of South Norway. Dr Sven Ekman has very kindly allowed me to use his list of the known records for Sweden, Lapland, and Finland, compiled from his own observations and from the literature. The years for Sweden south of lat. 66° N. are as follows: 1862-64, 1868-69, 1871-72, 1875-77, 1880, 1884, 1890, 1895, 1901.

These, except that recorded for 1880, all agree with the South Norway lemming-years within a year's variation either way. The exception may be due to the record not being made at the actual maximum, or it may be a real exception.

3. *Canada.*—The Barren Grounds of Canada are inhabited by lemmings of several species, chiefly the Hudson Bay Lemming (*Lemmus* (*Dicrostonyx*) *richardsoni*), and the Tawny Lemming (*L. trimucronatus*). There is practically no direct evidence as to the periodicity of their fluctuations, or details about them. But they are well known to fluctuate, and according to Rae (quoted by Barrett-Hamilton, 1910), the North American species migrate in certain years after the manner of the Norwegian species. There was a big migration

of Lemmus at Point Barrow, Alaska, in 1888 (Allen, 1903). However, we can attack the question from another angle.

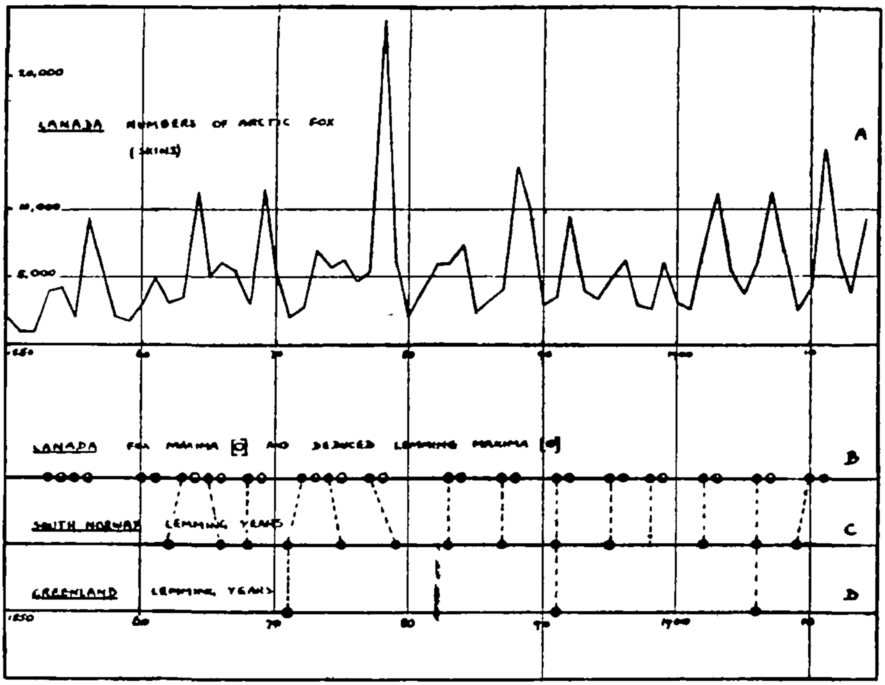


FIG. 2.—Years of lemming maxima in Canada, the mountains of South Norway, and Greenland. The years for Canada are deduced from the curve (A) of arctic fox skins taken annually by the Hudson Bay Company. (Data for Canada from Hewitt, 1921; for Norway from Collett, 1911; for Greenland from Winge, 1902, and Manniche, 1910).

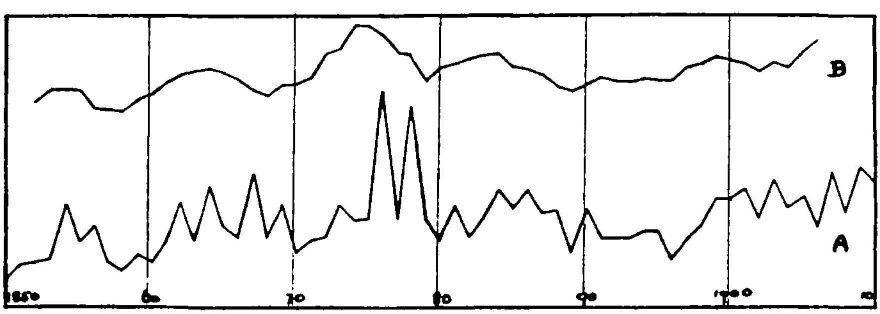


FIG. 3.—The curve A shows the effect of eliminating a period of 3·6 years in the curve of arctic fox skins (fig. 2 A). Curve B shows the effect of smoothing the lower curve (A) by taking 5-year averages for each year, *i.e.* two years before and two years after.

The lemming is the main source of food of the arctic fox; there is not the smallest doubt that the latter depends very largely on the lemming, just as its allies further south depend on hares, rabbits, and mice (Hewitt, 1921; Stefanssen, 1921). As will be shown later, the number of red foxes fluctuates with the number of rabbits (and probably mice), so we should expect the number of arctic fox to give a good indication of the number of lemmings. This is in fact so. The curve A in fig. 2 shows the variation from year to year of the number of arctic fox skins taken by the Hudson Bay Company (from Hewitt, 1921). If we plot the year before each fox maximum as in diagram B, we obtain the years when there was presumably a maximum of lemmings. The agreement with lemming-years in Norway is seen to be remarkable. In three cases the maximum in Canada occurs a year before, and in three cases a year after that in South Norway, so that the variations cancel out and leave us with the same mean period: 3.6 years. The reason why the maximum of fox skins occurs in the year after that of the lemmings is clearly shown by Manniche's study of a lemming-year in Greenland (Manniche, 1910). In the autumn of 1906 there were colossal numbers of lemmings, but these mostly disappeared before the winter was far advanced. He attributed this death to the cold early winter with little snow to protect the animals, but it is highly probable that disease was an important cause. The foxes swarmed in autumn, partly owing to immigration, but also presumably more young grew up successfully. They fed entirely on lemmings. But in the winter the lemmings had died or were inaccessible under the snow. Foxes make caches of lemmings for the winter (Hewitt, 1921), but by the spring these must have been used up, for Manniche was able to trap large numbers of foxes owing to their hunger. Now the Hudson Bay Company fur returns for any year include the catch of the winter before; in fact this is the main item, *i.e.* a maximum of skins in 1907 means many foxes caught in the winter 1906-1907, and in the spring. Such abundance will, of course, be the result of the year 1906, since arctic foxes mate in the spring and the young do not grow up until the autumn. So any abundance in fur returns for one year necessarily implies abundant food supply in the preceding year.

4. *Greenland.*—There are only incomplete data for Greenland, but the three certain years of lemming maxima, in every case accompanied by abundance of foxes, fit in remarkably well with the rest (diagram D, fig. 2).

5. *The Pribiloff Islands.*—Preble and MacAtee (1923) state: "As in other regions the lemmings of Saint George suffer considerable fluctuations in numbers." The data about years of abundance are not sufficiently definite to warrant any conclusions about the periodicity, but Elliot (1884) records them as very abundant in 1874, which agrees with Canada. He also states that there is a very marked variation in the severity of the climate with a period of about four or five years. This is only a rough estimate based on a year's stay and the accounts of the natives, and it is probably the 3.6-year period which is referred to. The results are very marked; the ice-pack may or may not stay round the islands in winter, and this influences the movements of the walrus, which in 1879-80 were driven south, with the result that most of the inhabitants starved. On the other hand some plants, *e.g.* Elymus, only ripens seed in the occasional warm summers.

6. *North Scandinavia.*—The foregoing account (section 1) only dealt with the mountains of southern Norway. It remains to consider the fluctuations of lemmings in the arctic regions of Scandinavia. Now the recorded lemming-years imply in every case that a migration of lemmings has taken place. It is obvious that the phenomenon of migration is far more striking than a mere increase in the numbers. The spectacle of processions of lemmings ecstatically throwing themselves over the ends of railway bridges, and falling to an apparently useless death below; the sea strewn with dead lemmings like leaves on the ground after a storm; lemmings making a bee-line across crowded traffic oblivious to danger; all these things are bound to make people talk. But in order that migration may be employed as a means of relieving congestion in an area, it is clearly necessary that there shall be somewhere to migrate to. In the mountains of southern Norway the lemming invades the lowlands. But up in the arctic regions the lemming-habitat runs down to

sea-level, so that there is no new land which it can occupy—only the snowfields on the mountains. It is probably for this reason that there are not much data about lemming-years in northern Norway and Sweden, and it seems likely that only in occasional years of great production does a migration take place. The absence of any very striking migration phenomena in Canada and Greenland confirms this idea. Rasmussen (1921), Winge (1902), Manniche (1910), and others record cases of lemmings migrating singly out over the sea-ice in definite directions; but the phenomenon is not a big one and never attains the same dimensions as in southern Norway. There is a possible explanation of this. In the arctic regions the enemies of lemmings are able to work day and night owing to the continuous summer daylight, whereas further south the lemming is protected by darkness to a large extent, and in fact comes out chiefly at night. This means that in arctic countries the enemies of lemmings will exercise a more efficient control over the numbers of the latter, and thus very excessive overproduction will be less likely.

So lemming-years in northern Norway are irregular, but when they do occur, always coincide with the southern ones within a year (1878, 1883, 1894, 1902, 1906).

The years which Dr Ekman has given me for northern Sweden are 1862-63, 1871-72, 1883, 1902-4, 1907, 1911, which also agree with the others within a year, either way, except that the one of 1902 apparently lasted three years.

7. *Finland.*—Dr Ekman's data also include some records of lemming-years for northern Finland. These are 1862-64, 1871-72, 1880, 1890-91, 1893 and 1895, 1902-4. These are not quite so regular but agree, except for 1880.

8. *Siberia.*—Allen (1903) says, of the lemmings (Lemmus and Dicrostonyx) of north-eastern Siberia, "the statements made by other writers concerning their comparative scarcity and abundance in different years are verified by the natives and whites here." No details of the years are given.

**Effect of Lemming Fluctuations.**—The lemming fluctuations have very powerful effects on the animals associated with them. This has already been shown for the arctic fox. In Norwegian lemming-years vast crowds of birds (owls, hawks, ravens, etc.), and mammals (stoats, foxes, etc.), are attracted to the mountains, and their numbers increase not only by their immigration but probably by their larger and more successful broods, due to the abundance of food. Similarly the arctic carnivores are profoundly affected. It is probable that many skuas and snowy owls (Manniche, 1910, etc.) only breed at all in lemming-years. There is not space here to follow out the readjustments of the food-cycle which result from the lemming-years. Two examples must suffice. The Short-eared Owl (*Asio flammeus*) collects in numbers and battens upon lemmings in South Norway lemming-years, and the Peregrine Falcon (*Falco peregrinus*), which hardly ever visits that country in normal years, comes and eats the owls (Berg, 1913). Again, in Greenland, an abundance of lemmings causes the arctic foxes to neglect other sources of food such as Ptarmigan and other birds. The latter accordingly increase. But in the next spring and summer, when there are few lemmings, these birds fare badly (Manniche, 1910).

**The Causes of Lemming Fluctuations.**—It is clear that the causes of these fluctuations might lie either with the lemmings themselves or with their environment. It is possible to conceive that there might be some rough natural period in the increase of lemmings' numbers (in the sense of having an increase in their "bank balance" of numbers every year), which was terminated after a few years by migration and disease following upon overpopulation, and that the population was thus reduced and the process started all over again. A little consideration will show that such an explanation of lemming periodicity is quite untenable. It is inconceivable that such a process could cause synchronised maxima on the various mountain blocks of southern Norway, which as far as lemmings are concerned, are isolated from one another, or again in the different districts of Scandinavia. When we find further that the lemming maxima are practically synchronous all over the arctic regions and the mountains of southern Scandinavia, any such "natural rhythm" becomes out of the question. Of course the natural rate of increase is a very fundamental factor in determining the size of periodicity into which the fluctuations will fit. The cause of the periodicity must therefore lie with the environment, and here the only possible factor which is acting in a similar way all over these regions is climate. We do not know how this climatic factor acts, whether directly, or indirectly through plants, or other animals, but there can hardly be any doubt that we have here to look for a periodic climatic effect whose period is about 3.6 years on the average, and which acts over the whole of the arctic regions and in the Norwegian mountains. It will be shown later that it probably occurs in temperate regions also.

The curve of the arctic fox skins (fig. 2) shows on casual inspection no distinct traces of any other periodicity besides the short 3.6-year one. But if the effects of this periodicity are eliminated interesting results are obtained. I am much indebted to Mr G. M. B. Dobson for showing me the method of carrying out this elimination (due to the late Prof. Chrystal), and for actually demonstrating the existence of other periodicities underlying the 3.6-year one in the fox curve. The method is graphic and consists essentially in shifting the curve half a period (in this case 1.8 years) to one side, and making a new curve based on the means of these two superimposed curves. In this way the 3.6-year period is largely eliminated, but the method is only absolutely accurate in the case of a regular symmetrical curve. It will be seen in fig. 3 that there is left a curve which is irregular in detail, but which shows a well-marked 10 to 11-year period. This comes out more clearly if 5-year averages are taken (upper curve in fig. 3). This agrees with the period found among so many of the southern animals (Canadian rabbit, etc.), which are discussed later.

I shall attempt to show that the 10 to 11-year period of the rabbit may be due primarily to the 11-year period in the sun. If this is so, the fox curve indicates that the solar period is having a slight effect in the arctic regions. This agrees with the conclusion reached from other evidence, that the effect of the solar variation is greatest in the tropics and gets fainter farther from the equator. It will be seen that there is no known cause for this well-marked $3\frac{1}{2}$-year period in the arctic climate. It might be caused by some short period in the sun, or by some unknown terrestrial factor, or the complicated interaction of several such factors.

Since the curve for the arctic fox shows a well-marked 3.6-year periodicity with a less distinct 10 or 11-year period underlying it, it might be thought probable that the curve for the numbers of the southern red fox, which shows a definite periodicity of about ten years, would have a concealed short

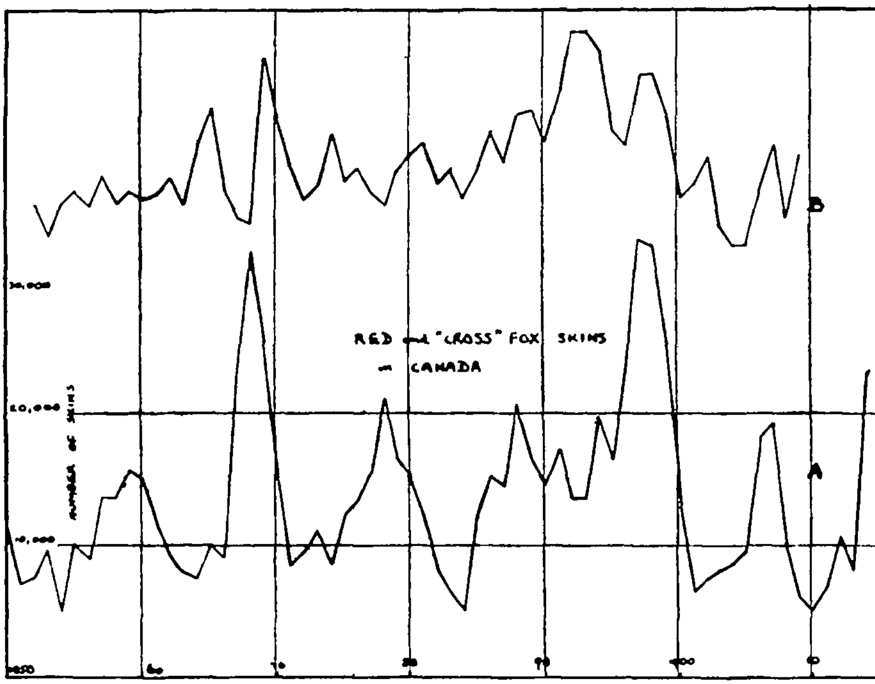


FIG. 4.—Curve A shows the numbers of red fox and "cross" fox taken by the Hudson Bay Company in Canada each year. Curve B shows the same curve after a period of 10 years has been eliminated from it. The period remaining is one of about 3½ years.

period. This is found to be the case. Curve A, fig. 4, shows the number of red fox, and the variety known as the cross fox, taken from year to year in Canada (Hewitt, 1921). Curve B shows the effect of eliminating a period of ten years from the curve. There is left a well-marked short period of about 3½ years which resembles the arctic fox curve (fig. 1A). The comparatively rough method of analysis does not allow of an accurate comparison being made. Now the southern fox feeds both on rabbits and mice. The rabbits cause the 10-year period in the fox, and it is shown later that there is a short period of 3½ years in Norwegian mice. It is very probable that the short period in the red fox curve is caused by variations in the supply of mice in Canada. It might also be caused by climate acting directly; but the absence of any such period in the lynx curve goes against this idea, since the lynx eats rabbits only. In any case the ultimate cause must be climate.

It appears then that there are two periods in the numbers of foxes and their food, and that the effects of the shorter one are more marked in the arctic, while those of the longer one are more marked in the temperate regions. This difference must be to a large extent due to the difference in prey, *i.e.*

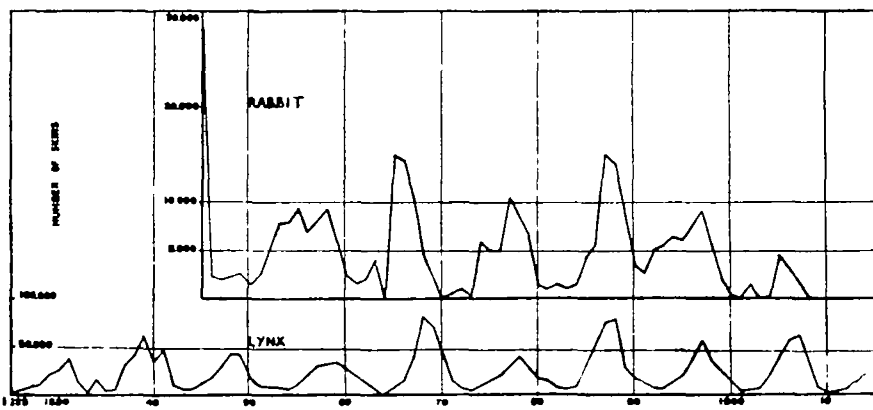


FIG. 5.—Curves show the number of skins of Canadian rabbit (varying hare) and lynx taken annually by the Hudson Bay Company (from Hewitt, 1921).

lemmings in the one place and mice and rabbits in the other, but the climatic difference may also be of the same nature.

Finally, it should be noted that the lemming differs from most of the other fluctuating rodents in that it does not have more young in a brood in good years; it probably has more broods in a given time, and the young grow up more successfully under the good conditions.

**The Varying Hare.**—The violent fluctuations in the numbers of the Canadian rabbit or varying hare (*Lepus americanus*) are well known through the writings of Seton (1920), Hewitt (1921), Preble (1908), and others. About every ten years the numbers of the rabbits increase to a maximum, just as in the shorter cycle of the lemmings, and then almost the entire population is killed off by an epidemic disease. The fur returns of the Hudson Bay Company given in Hewitt's book, form a good record of these fluctuations since the year 1845 (fig. 5).

As will be seen there is an average periodicity of about ten years between 1845 and 1905. The next maximum was in 1914 (Hewitt, 1921). The returns include partly the year before, and it is not possible to say in which year each maximum really came; but as the method of collecting is the same throughout, we can compare the different parts of the curve with each other. The curve of course represents the total for the whole country; but the maxima do not occur in the same year in all parts of the country (although there is only a variation of a few years, otherwise there would not be these regular maxima shown by the totals). The curve of numbers for a single district, *e.g.* the Mackenzie River region, would be far less symmetrical, showing a very steep drop after the year of maximum. It seems well established that the number of young in a brood and the number of broods in a season vary according to the year in the cycle. In years of maximum abundance there are eight to ten in a brood and two or three broods in a year. In bad years there are three in a brood, and only one brood in the season. This fact at once marks off the whole phenomenon as something more than a cycle due to the time taken by the rabbits to increase after decimation by an epidemic. The process must be extraordinarily regular, for the Indians of the Athabasca-Mackenzie region are in the habit of counting the numbers of embryos in the rabbits which they catch, in order to get an idea of what the rabbit "crop" is going to be like in the next year (Preble, 1908). This cycle of reproductive activity has been treated so far as a mysterious thing, usually attributed to some obscure "physiological rhythm." There is nothing in physiology which offers the remotest suggestion that any such cycle (considered as an independent rhythm going on in the animals) could possibly exist. When we reflect that the rhythm would have to act in a mixed population of animals of all ages, and through several generations, and more or less simultaneously (within a few years) all over Canada, such an explanation becomes increasingly unlikely. And what is more it is quite unnecessary. The facts could quite easily be accounted for by variations in the conditions under which the animals live. Now we know that there are periodic climatic changes going on in North America with about the same period as that of the rabbit-fluctuations (*cf.* the Sequoia evidence, and Küllmer's shift of the storm tracks). So it seems impossible to escape the conclusion that the cycle in reproductive capacity and numbers is caused by some climatic cycle which varies the conditions. Increased young and more broods might be due to better food supply (climate acting through plants). The evidence about mice suggests that this is an important factor. Better conditions in the physical environment (temperature, evaporation, etc.) might produce the same result. The fact is, we know very little about the physiology of reproduction in this species, and not much about that of any mammals. All that can be said, and that can be said with some certainty, is that the variations in reproductive capacity, and consequently in numbers of this rabbit from year to year, are due directly or indirectly to variations in climate. The period of ten or eleven years at once suggests that of the sun, since it is fairly certain that the latter has some effect on the climate of North America. The chief objection raised by meteorologists against the existence of such climatic periods dependent on the sun is that the effects would be too small to be of importance. But in addition to the fact already pointed out, that what is small meteorologically is often of very great importance biologically; it should be remembered that in the discussions on the subject, the *direct* effect of sunlight is usually left out, chiefly because the technique for measuring it is still in an early stage. Sunlight is of immense importance to plant-life (probably more as to number of hours than as to intensity). In any solar variation the light must vary with the other things, and it is perfectly possible, indeed likely, that the 11-year variation in the sun produces effects by this means, on plants and therefore indirectly upon animals.

Fig. 6 shows all the maxima since 1845, marked on the sunspot curve. It will be seen that there is a rabbit maximum just before or on, or just after each sunspot minimum, except in 1905, when there was a small maximum near the sunspot maximum. In other words, in one of the sunspot periods during this time there were two rabbit maxima instead of one. It will also be noticed that the rabbit maximum comes nearer the sunspot minimum after an unusually high sunspot maximum preceding it. This may indicate that worse weather resulting from a high maximum causes the recovery in numbers of rabbits to take a year or two longer.

Now though the rabbit maximum of 1905 does not agree with the sunspot curve, fig. 1 shows that it follows the curve of average earth-temperature, just in the same way as former maxima. In other words, the curve of earth-temperature falls abruptly two or three years before its usual time, and this appears to be explained by the volcanic eruptions of 1902 and 1903. This idea is confirmed by the marked drop in the

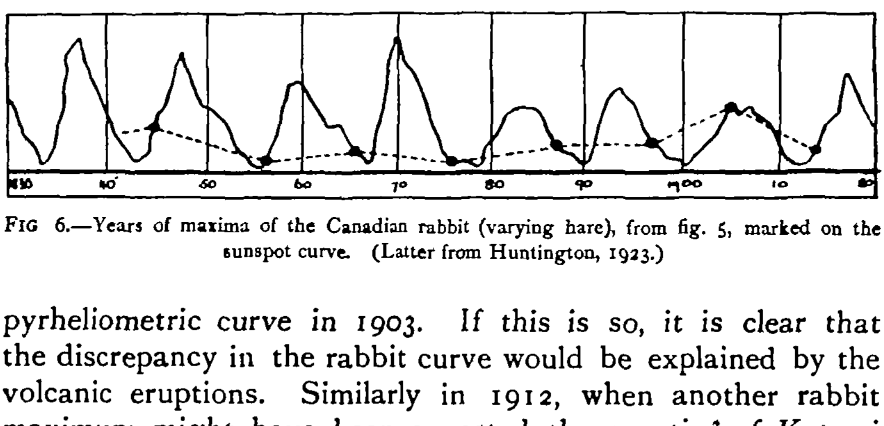


FIG 6.—Years of maxima of the Canadian rabbit (varying hare), from fig. 5, marked on the sunspot curve. (Latter from Huntington, 1923.)

pyrheliometric curve in 1903. If this is so, it is clear that the discrepancy in the rabbit curve would be explained by the volcanic eruptions. Similarly in 1912, when another rabbit maximum might have been expected, the eruption of Katmai occurred and caused another sudden drop in earth-temperature, which soon recovered, so that the maximum of rabbits came in 1914. This hypothesis, for of course it is at present nothing more, does seem to cover the facts, and its truth will be tested by the relations of later rabbit maxima to the sunspot and earth-temperature curves. It is worth noting that the 1905 rabbit maximum for the whole of Canada was a very small one; locally, however, the rabbits reached their customary vast numbers, so the area in which it took place must have been smaller than usual. If we allow for the irregularity in 1905, the rabbit period agrees very well with that of the sunspots: *i.e.* omitting the one in 1905, the average period for rabbits between 1845 and 1914 is 11.5. But the 1914 one should have been in 1912, and this brings the average to 11.1, which is about that of the sunspots (= 11.2). These fluctuations in the numbers of rabbits have an immense influence on the numbers of the carnivorous animals which live on them. This is well shown by the curve for lynx numbers (fig. 5). Owing to the fact that the lynx migrates about over great distances in search of food, its curve is much smoother than that of the rabbits. There is a delay of from one to three years in the effects of rabbits on lynxes, caused by factors in the trapping which are fully explained by Hewitt (1921).

A similar fluctuation occurs among other animals that eat rabbits: the red fox and its varieties the black and cross fox, the martin, etc. The fox curve has already been discussed, and it will be remembered that it showed a short period of 3½ years as well as that due to the rabbits. It is important that the rabbit curve itself when analysed shows no regular underlying short period, but only quite irregular variations. So the short period of the fox must have some other cause. This might be either the fluctuations of mice which form part of its food, or some direct effect of climate, *e.g.* hard winters.

**Other Rabbits and Hares.**—Among all the species of rabbits, jack-rabbits, and hares, there exists the same phenomenon of periodic increase followed by epidemics which kill off most of the population. Palmer (1896) states that the jack-rabbits of the U.S.A. (really hares; known as "narrow-gauge mules" in California) have comparatively few natural enemies, and that their checks are lack of food, climate, and disease. In some cases migration takes place; *e.g.* Anthony has recently noted that the Little Chief hare (Ochotona) has periodic emigrations in America. Other references to such periodicities are contained in the works of Howell (1923), Nelson (1909), Bailey (1905).

The data about the actual years of maxima are too scanty and casual to allow any safe conclusions to be drawn about the length of the period in these species.

**Mice.**—Plagues of mice have often been recorded in ancient times, in various parts of the world, and these are due to abnormal increase in numbers similar to that found among the rabbit and lemmings. A vivid description is given by Holinshed of a mouse plague which took place in 1581 in Essex (quoted by Maxwell, 1893). Similar bad plagues occurred in Scotland in 1892-93, when the mice destroyed the grass on wide areas of hill pasture (Harting, 1892; Maxwell, 1893). The abundance of mice attracted large crowds of kestrels and short-eared owls. These are always looked on as saviours of the farmer, though as a matter of fact they only prolong the plague by keeping the numbers of mice down below the density necessary to cause an epidemic.

Plagues of this type of course cause enough damage to attract attention, and so they are recorded. But where the increase is less marked we have not usually any record. Even where the increase has been reported, the species of mouse has often not been identified. In addition mice are not so conspicuous as their larger allies; there are no commercial records of skins, and no regular migration-phenomena as in the lemmings.

It follows from this that, although the periodic increase of mice has attracted general attention throughout history, there is not the same favourable material for analysing the periodicity as in some of the other rodents. But the data, though scattered, are sufficient to make it clear that a definite periodicity exists, and that the fluctuations are due to climate. The following are the main points:—

1. Mouse plagues in Great Britain. The species of mouse which is usually responsible for plagues in England and Scotland is the short-tailed field mouse or common grass mouse (*Microtus hirtus*). But other species are often abundant at the same time as it, e.g. the long-tailed field mouse (*Apodemus sylvaticus*) and the bank vole (*Euotomys glareolus*). But the first is the species which is usually in question when "vole plagues" are spoken of. As has been mentioned, the records of plagues are only indicators of unusually big increase, and therefore provide only incomplete data for working out the periodicities. They are to be compared with the lemming-years of northern Scandinavia, which come only at irregular intervals, while there is almost certainly a regular periodicity

in numbers which, however, does not always become sufficiently marked to be noticed. With this reservation in mind we may examine the data of mouse-plagues in this country. Fig. 7 shows the years in which any mouse plague has been recorded in any part of Great Britain. The full details of localities are to be found in Barrett-Hamilton (1910), except that of 1923 which I have on the information of Dr Longstaff. The latter will be referred to again later, since it furnishes an important clue to the way in which the plagues come about. In every case except 1900 the species mainly or wholly responsible was the short-tailed field mouse. In 1900 the records are of the other two species. It is plain from the diagram that mouse plagues have occurred about every eleven

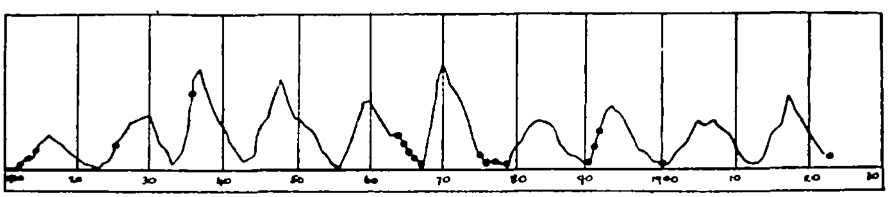

FIG. 7.—Recorded years of mouse plagues in Great Britain, marked on the sunspot curve. (Mouse data up to 1900 from Barrett-Hamilton, 1910; the one in 1923 from Dr Longstaff; sunspot curve from Huntington, 1923.) Allowance has to be made for the delayed effect of the climatic factor, as in the case of beech-mast (see p. 22).

years or multiple of eleven years, and that they seem to come round about the sunspot minimum. This is, of course, only an indication and does not prove much. But in view of other evidence we may say that there is usually a marked maximum in the numbers of mice somewhere every eleven years or so.

2. It is important to find out in what way climate affects mice, and how it can control their numbers. The year may be divided into two sections as far as mice (or indeed almost any animals) are concerned. Firstly, the breeding season, when the animals are increasing in numbers and are also being reduced by checks. Secondly, the non-breeding season (autumn and winter), when there is no increase to counterbalance the mortality. There will be a certain number of mice in any one district in autumn, and this number is the resultant of rate of increase as balanced against mortality through checks. In spring there are a certain number left,

after the checks of the winter. Now the essential thing in determining whether there is a fluctuation over a series of years is increase or decrease in the latter number. Better conditions in summer with slightly worse winter conditions would have the same result as worse conditions in summer and much better ones in winter. But if both improve simultaneously there is bound to be an increase in numbers. Now in the case of the mice there are four main factors which are thought to affect them in an important way. Firstly, mild winters favour them, and leave a larger stock to start the next season's population. Secondly, better physical conditions during the breeding season. Thirdly, abundant food supply at any time, but especially in the breeding season. This would be the effect of climate favouring plant life in some way, *e.g.* big crops of beech-mast or acorns. Fourthly, a favourable growing season leaves plenty of plant cover in the winter, which gives the mice protection from their enemies. There must, of course, be other factors as well. But the point is that not only are all these factors connected with climate, but the last three are all the result of the same kind of climatic complex during the breeding season.

Dr T. G. Longstaff has kindly given me some notes on a mouse plague in the New Forest, and the conditions accompanying it. In 1921 there was a very dry and hot year, which evidently caused the beech flowers to form very successfully in autumn, so that in the autumn of 1922 there was a colossal crop of beech-mast. In the spring of 1923 the woods were carpeted with sheets of beech-seedlings, and in May, June, and July there was a plague of mice in the district near by (long- and short-tailed field mice). They were found dead in large numbers at the end of this time, evidently killed by an epidemic. Now the winters over this period were all mild, and this apparently combined with the delayed effect of the 1921 summer in making a good food supply, to cause a great increase in the numbers of mice, which eat beech-mast among other things. The chances are that other plants prospered in the same way as the beech, and so the other foods may have been more abundant too.

The scattered notes on the subject in the phenological reports of the *Quarterly Journal of the Meteorological Society* show that there has been an unusually heavy beech-mast crop in Britain every eleven years.

Enormous crops: 1900, 1902, 1911, 1912, 1922. (Crops larger than usual, but not nearly as big as these, occurred in 1896, 1905, in places.)

The records do not go back with any completeness beyond this point.

This periodicity in beech crops is suggestive, but there are not sufficient records to prove the hypothesis that the crops are correlated with the sunspot cycle.

The great mouse plague in southern Scotland in 1892-93 was associated with mild winters and "growthy" summers; the grass crops were unusually fine until the mice ate them up.

3. In several cases these big mouse plagues have happened simultaneously in different parts of the world. This is clear if we take the regions for which there are good records:—

1875: The Athabasca-Mackenzie ("A-M") region in northern America (Preble, 1908); South Scotland (Harting, 1892; Maxwell, 1893); Galicia and Hungary (Maxwell, 1893); Norway (Collett, 1911).

1891-93: The A-M region; South Scotland; Norway; Thessaly (Maxwell, 1893).

1900: The A-M region; England (Barrett-Hamilton, 1910).

Such facts would be explained by the hypothesis that there was some climatic factor acting widely, such as that caused by solar changes.

4. If these mouse fluctuations depend to any large extent on the solar variations, then they should conform to the map given by Walker (1923) which divides the world into areas according to the way in which they act with reference to the sunspots. Though the data are very scanty, the mouse years do in fact agree with this map. (In Norway, however, a shorter period occurs, of 3½ years. See next section.)

All the places mentioned above have more rain and storms at sunspot maxima. On the other hand, the only mouse plague which I can find that occurred at a sunspot maximum is that recorded by Hudson (1892) in La Plata in 1872-73. Now this area is one of those which have more rain and storm at minima. So the facts, as far as they go, do not conflict with the idea that the mouse periodicity is under the control of the solar variation.

5. The curves given on p. 17 show that there is a short period in the numbers of foxes in temperate North America, of about 3½ years. It was suggested that this was due to fluctuations in the numbers of mice, which might have a period of that length. There is evidence in support of this, from Norway. There, various species of mice occur in unusually large numbers in the lowlands and also in the mountains in the same year as, or within a year of the lemming maxima, in one place or another. The following years are given by Collett (1911):—

*Euotomys glareolus* (bank vole): 1887, 1903, 1906.
*E. rutilus:* 1876, 1880, 1883, 1903, 1906-7, 1910.
*E. rufocanus:* 1872, 1876, 1880, 1887, 1904, 1907.
*Microtus agrestis* (short-tailed field mouse): 1876, 1880, 1882-83, 1887-88, 1891, 1894-95, 1897, 1906.
*M. ratticeps:* 1863, 1872, 1876, 1891, 1894-95, 1897, 1906.

Thus in or within a year of every lemming maximum there has been an abundance of from two to four species of mice. This suggests the probability that there is a 3½-year period in the numbers of mice, but that increase in some places, *e.g.* England, never reaches the dimensions of a "plague," unless the additional force of some longer period is added. Whereas the 11-year period acts only faintly on the lemmings in the arctic, it is much more strongly marked farther south, and may well affect the mouse numbers in this way. Perhaps such a hypothesis sounds rather too rigid, but then no one would ever have believed that rabbits and lemmings could behave with such clockwork regularity.

6. We have not got direct evidence that the number of young in a brood varies according to the year, as in rabbits,

but there is indirect evidence. It is noticeable that in all the text-books (Barrett-Hamilton, 1910, etc.) the mice are said to have about twice as many mammæ as they have young in brood. Thus the bank vole, short-tailed field mouse, and dormouse have eight mammæ, while the usual number of young is four, five, four respectively. The long-tailed field mouse has six mammæ and four or five young. This is explained if we assume that like the rabbit their number in a brood goes up to double in good seasons.

**Results of Mouse Fluctuations.**—One of the most striking and universal results is that the short-eared owl (*Asio flammeus*) very soon turns up and gorges on the mice. The owls often stop on migration at places which they do not visit in ordinary times at all. The number of eggs in a clutch in these years is nine to fourteen instead of four to eight, and they have two broods instead of one in the season. This gathering of the owls has been recorded from South America (Hudson, 1892), Texas (Bailey, 1905), Canada (Hewitt, 1921), Britain (Barrett-Hamilton, 1910; Harting, 1892), Norway (Collett, 1911; Berg, 1913).

It seems likely that the fluctuations in the numbers of mice must have very important effects on the regeneration of forest trees. Watt (1923) has shown by experiment that in a normal year, when the beech-mast crop is small, *e.g.* 1921, about 98 per cent. of it is eaten up by mice before it has a chance to germinate at all. That which does germinate succumbs to the attacks of mice plus a great many other enemies. In a year like 1922 when there was an enormous crop, only about 40 per cent. was found to be eaten by mice before germination had time to start. If the numbers of mice remained constant, the thing would be comparatively simple. But as we have seen, they do not remain constant. What happens seems to be this. There is a huge supply of food in the beech-woods in autumn, and this attracts a big crowd of mice from round about, as well as the original population. They are able to survive the winter better, owing to its mildness, and to the abundant food supply, but do not succeed in eating all the beech-nuts by the spring. The tree has thus got ahead up to this point, and as a result we have the sheets of seedlings in the woods. The mice now increase to such an extent that an epidemic results, and most of them are killed off. From the point of view of the tree, the sacrifice of half its seed crop has caused the mice to increase too much and die off, thus removing the danger to its seedlings to a large degree. Whether this has actually evolved as an adaptation, or occurred ready-made, there is no doubt that this certainly acts as an adaptation for the tree.

Rodents are evidently a big factor in affecting the natural regeneration of forest trees. Similar relations between good years and heavy crops are found for the oak. In this case the big crop often comes in the year before that of the beech, but also sometimes in the same year. Here also the mice must be an important factor, since they feed extensively on acorns. The hornbeam also has periodic heavy crops in England, after the manner of beech (Christy, 1924). Pearson (1923) states of the Western Yellow Pine in America that in ordinary years rodents eat up the entire seed-crop, but in good years some is left over. In all such cases the tree has to have a much bigger excess of seed than might be supposed, owing to increase in the mice as well. Show (1924) says also that rodents almost defeated attempts at artificial sowing of pines in California. A further complication exists in some cases, for according to Hofman (1920) rodents aid the regeneration of the Western Yellow Pine and the Douglas Fir in North America by making many caches of seeds in the ground, which get forgotten. When the forest is cut or burnt, and regeneration occurs, these caches play a large part in causing the Douglas Fir to prevail over other trees owing to the abundance of "planted" seeds.

**Other Mice.**—There is evidence of periodic fluctuations in the numbers of a good many species of mice besides those already mentioned.

Deer-mice (Peromyscus), and jumping mice in North America (Howell, 1923).

The Texas cotton rat (*Sigmodon hispidus*), which had tremendous invasions of neighbouring regions in 1854 and 1889-90, and attracted vast crowds of hawks, owls, skunks, weasels, snakes, etc. (Bailey, 1905).

The Baird wood-rat (*Neotoma micropus*) of Texas and Mexico (Preble, 1908).

The bushy-tailed wood-rat (*N. cinerea occidentalis*) in Northern America (Anthony, 1923).

The water-rat in Britain and Norway (Barrett-Hamilton, 1910; Collett, 1911).

It is pretty clear from what has been said that mice do fluctuate in numbers periodically, and that this is due to climatic variations. Further work is required before we can say definitely what the exact periodicities are in each case.

**Other Rodents.**—Periodic fluctuations occur among some other species. The musk-rat curve of skins (Canada) shows a short 3 or 4-year period mainly. Seton says that these fluctuations are probably related in the main to the amount of water "which, as is well known, is cyclic in the North-West" (Seton, 1920). The difference between a good and a bad year must be enormous, for he mentions that they used to catch twenty musk-rats in an hour after sundown in 1900 in the Mackenzie region; in 1907 only seventeen were seen in six months. He also states that red squirrels fluctuate like the musk-rat. Anthony (1923) says that the Yellow-bellied Wood-chick (*Marmota flaviventer*) of the U.S.A. has emigrations at certain times. No doubt many other species will be found to fluctuate in numbers, when naturalists have got rid of the obsession that numbers always stay constant.

The beaver forms an interesting exception to the other rodents. The Hudson Bay Company fur records show that the beaver does not have any regular short periodicity in its numbers, although there is a general "secular" trend in the curve depending on the gradual exploitation of the country followed by exhaustion of the stock of beavers. Now the beaver does not depend on the yearly income of plant-food which is rescued by plants out of the sun's radiation. It eats the bark of trees almost entirely, and when the trees are used up in the neighbourhood of its colony, it moves on somewhere else. Thus the beaver leads an ideal existence, living entirely on capital. What is more, it regulates its water-supply by building dams, and so is to a large extent independent of variations in rainfall, unlike the musk-rat. Also its aquatic life in stream conditions causes it to live to a large extent in water with a constant temperature Bailey states that there is never any overcrowding in beaver colonies, and that disease seems to be unknown among them (Bailey, 1922). Further, there are four mammæ in the female, and the normal number of young is four. There are certain enemies which act as checks, but a very important factor in regulating the numbers is rivalry among the males. The

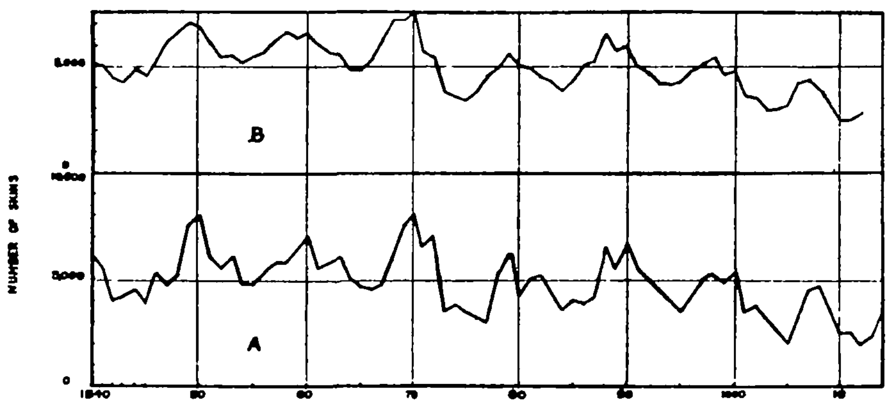


FIG. 8.—Curve A shows number of skins of the fisher taken annually by the Hudson Bay Company in Canada (from Hewitt, 1921). Curve B shows the effect of eliminating a 3.6-year period in Curve A. Note the almost smooth 10 to 11-year period.

beaver is polygamous and there are severe fights among the males for possession of the females. We see, then, in the beaver an animal which has so regulated its existence that it is independent of short-period climatic variations. Whether this is an advantage in the long run is another matter, which will be gone into later on.

**Other Mammals.**—The fisher, which is a near relation of the martin, but has a much more general diet of all kinds of other animals, has a well-marked periodicity, shown by the Canadian fur returns (Hewitt, 1921). Fig. 8 shows that the curve is rather irregular, but has a general 10-year periodicity corresponding to that of the rabbit. But as the rabbit is not the main source of its food, it is plain that the same climatic influence must be affecting the other animals on which the fisher preys. Fig. 8 also shows the effect of assuming a periodicity of 3.6 years and eliminating it. The 10-year curve comes out quite smooth, except in the early part of the nineteenth century, when the fur returns are not so regular. This proves that there is a short period present, but as to its cause we are in ignorance.

The mink and wolverine have curves which resemble that of the fisher, showing well-marked periods of about $3\frac{1}{2}$ and 10 to 11 years. That of the wolverine is not, however, so clear as the others, since the numbers taken are not very large.

The skunk has a conspicuous 10 to 11-year period, but no clear short period. Like the fisher, the skunk has a wide range of food, so that the fluctuations in its numbers must be caused by fluctuations among many other animals, or else by the direct effects of climatic variations, or by both. Periodic abundance of shrews (*Sorex araneus*) is also recorded by Collett, for Norway (Collett, 1911).

The mouse marsupial, *Sminthopsis crassicaudata*, which inhabits the deserts of Australia, has ten young in a brood in good years (i.e. wet ones), and only four or five in bad (i.e. dry) ones (Buxton, 1923).

We have seen that the numbers of many different orders of mammals fluctuate in a periodic way, and the phenomenon is obviously of wide occurrence in mammals. The rodents show it most clearly, but it occurs as well in insectivores, carnivores, and marsupials. Further work will, no doubt, disclose its existence in other groups of mammals.

**Birds.**—Pallas's Sandgrouse (*Syrrhaptes paradoxus*).—This species lives in the sandy deserts of Central Asia, e.g. the Gobi Desert, where it depends for food on the salt-soil plants. Periodically the sandgrouse leaves its usual home and migrates in large numbers into China on the east, and Europe on the west. The bird is a very strong flyer, and is recorded periodically from the British Isles. These records give a delicate index of the years of maximum exodus from Asia. There has been a very big invasion every 22.5 years on the average, the years being 1863, 1888, 1908 (Witherby, 1920). There have been minor invasions as well, and these were in (1872), 1876 (1889, 1890, 1891), 1899 (1904, 1906, 1909). Of the two in 1872 and 1876, the latter was the greater, so that 1876 and 1899 are to be considered as minor maxima, while the others (in brackets) are clearly associated with the big years, *i.e.* form part of the same maximum. There was apparently no visit in 1918 or 1919.

It seems that there is an invasion usually every eleven years or so, while every alternate one is very big. We should expect another big visit about 1930. The cause of the invasion appears to be the onset of glaze-frosts or heavy snow in early spring, which prevent the birds from getting at their food (Dresser, 1871). This of course constitutes relative overpopulation. The net result of the whole phenomenon is that thousands of birds perish, and this is precisely the same result as when rabbits increase in numbers and die from disease, or when lemmings trek out of their usual habitat and are destroyed.

The average period of the sandgrouse maxima is 11.2 years, which is exactly that of the sunspots. Whether the 22.5-year period is anything to do with the change in magnetic polarity of the sunspots it is difficult to say!

**Other Birds.**—The bird-census work recently started in the U.S.A. seems to show that the numbers of birds fluctuate in a regular way. Both in Europe and America the bad winter of 1917-18 killed enormous numbers of small birds, and it was not until 1920-22 that they recovered their former numbers. This is proved by actual census figures for the U.S.A., 1916-20 (Cooke, 1923). There are numerous other birds which have big invasions of neighbouring countries at intervals. Among others may be mentioned the Waxwing, Mealy Redpoll, Crossbill (Witherby, 1920); and the Nutcracker (Simroth, 1908; Blasius, 1886). The Siberian race of the Nutcracker invades Europe in particularly large numbers every ten to eleven years, or every twenty to twenty-two years, like the Sandgrouse, *e.g.* 1844, 1864, 1885, 1896, 1907. Simroth has pointed out that this is correlated with the sunspot cycle. The periodic increase of owls, hawks, and skuas has already been pointed out. De Lary (1923) states that the cuckoo and some other birds vary in their dates of arrival in France in spring according to the sunspot cycle.

**Insects.**—Periodic variations in the numbers of insects are well known, and may either be caused by over-increase of individuals, leading to migration and subsequent destruction, or else under-production of food leading to the same thing. In both cases the migrants usually perish, and the net result is the same as if they had been wiped out by disease. The best-known examples are found among butterflies (Poulton and Walker, 1921; Walker, 1914), and in the locust family (Uvarov, 1923). Unfortunately, although in most cases the migration must be due to some climatic cause, and can sometimes be proved to be so, the periodicities are not well known. In the case of the locust the only records of such things are the invasions of other countries. Now insects always depend on the direction of the wind in their migrations, flying either with, against, or obliquely to it. The result is that a regular periodic migration from one centre appears as irregular invasion when considered from the point of view of the country invaded, since the wind may be different at different migration times, and the countries visited therefore different (cf. the confused results of trying to analyse locust visitations on this method, by Kulagin, 1921). But it is also significant that mammals and birds do show much more clearly than other animals the effects of 3 to 10-year climatic variations. This may be because they have temperature regulation, and therefore are not affected so much by chance weather variations, such as sudden hard frost for a day. Insects and other cold-blooded animals are much more at the mercy of these kind of variations. Mammals and birds "smooth" these minor variations from day to day and month to month, and therefore give an average result for the whole year.

But whether insects and other cold-blooded animals really have regular fluctuations or not, they must be strongly affected, firstly by these short-period climatic variations, and secondly, by the direct and indirect results of the fluctuations of the other animals, which must have profound effects ecologically. Finally, as examples of the same kind of thing in widely different groups, one may mention the periodic invasion of freshwater regions by the shipworm (*Teredo navalis*) during very dry summers in Holland, in 1730-32, 1770, 1827, 1858-59 (Kofoid, 1921); also the correlation between the moon and herrings' movements (see p. 122), and between periodic snowfall variation in Norway and fishery results (Sund, 1924). There is also to be considered the yearly fluctuation of most animals, which may have effects similar to the larger ones. For instance, *Daphnia pulex* forms large numbers of winter eggs in the autumn, only a few of which succeed in hatching in spring to start the next year's stock. These, and irregular fluctuations, are just as important as the others, biologically, though less so from the point of view of meteorology.

## 4. Discussion.

We have already shown some of the economic consequences of these fluctuations in the numbers of animals. It is of vital interest to the forester to know the relations between rodents and the germination and survival of tree-seedlings; the possibility of predicting the years in which plagues of mice will occur may affect him enormously. Again, in the fur industry, efficient prediction of the number of skins which will be obtained is of importance. In particular, however, the meteorologist and the geophysicist are provided with a new method of getting at the facts of climatic cycles. Considering what comparatively good results can be obtained from the correlation of facts which have usually been recorded on account of their intrinsic interest, or because they touched the pocket of the observer, it should be possible to attain much more complete knowledge of these things if systematic observations were started. The idea of using animals and plants as indicators of climatic events is of course an old one. Since about 1870 the Royal Meteorological Society has carried out systematic phenological observations, published each year in the journal of that society. But the notes have been almost confined to records of first flowering and first arrivals of migratory birds, etc. Many of these do not sum up climate any better than a meteorologist can. Many of the occurrences such as the opening of flowers depend on single environmental factors, e.g. the snowdrop (*Galanthus nivalis*) opens when the temperature rises above 10° C. and the hive-bee sallies forth at the same temperature (Church, 1908). Thermometer readings would tell one just as much as these observations, and more accurately. Now the only point in using animals and plants in meteorology is because they are capable of integrating and accumulating the factors of climate to a large extent; these integrations are not, however, shown by the kind of phenomena which are usually recorded, for the reason given above, and also because of the exceptional cases which give a false idea even of the simple weather events. But when we consider the rate of growth and reproduction of animals it is clear that we are dealing with quite a different kind of weather indicator. The rate of metabolism is altered by all kinds of different factors, and the end-result may be the same, e.g. dry winds causing evaporation might have the same effect as lower temperature. So the first point is that we are dealing with a rate of something happening, instead of with a single event, and that the rate depends on the combined integrated effects of a great many environmental factors. The second point is that we are dealing with a geometrical rate of increase or varying acceleration of a rate. The result is that the climatic variations are shown in a highly magnified way. Variations in meteorological factors (e.g. comparisons between average rainfall at sunspot maxima and minima) are always very small when measured directly; the climatic effects are the result of these small differences accumulating.

The fluctuations in the numbers of animals may be compared to the beam of light which is used to magnify the small angular variations of a fine galvanometer; the original variation is shown on an exaggerated scale.

Plants do not give such good records because they are mostly longer lived and therefore the regulation of their numbers is quite different. We do get variations in the rate of growth shown well in the annual rings of trees, but not in the immensely magnified form found in the variations in number of animals.

But among the most important consequences of these fluctuation phenomena are their effects on evolution and other biological questions, and it is with these that we shall now deal. The conclusions that follow do not depend for their validity on the truth or otherwise of the hypotheses that have been advanced in this paper to account for the fluctuations in the numbers of animals. They follow from the fact of fluctuation, and about this there is not the slightest doubt.

The amount of fluctuation varies widely in different animals, and may in some cases be practically nil, as in the beaver. But among a great number of species, variation in numbers plays a big part in their lives, and it is with these species alone that we shall be concerned, in what follows. The climatic theory of the cause of animal fluctuations has this significance, if it be accepted: it means that these short-period variations of climate have been causing similar phenomena during the whole time of the evolution of life on the earth. For the causes of these variations have almost certainly been in existence during the whole of this time (the Sequoia record, and Chinese observations carry the sunspot variation certainly back four thousand years, and there is no reason to believe that they were ever absent before that time. Also the astronomers are agreed on this point, on general grounds.)

A knowledge of the animal periodicity alone, puts us in a position to study natural selection in action in the field, since if we know within a year or two when the critical period for the animal will be; it is possible to arrange intensive field-work. This subject could be profitably taken up by ecologists, since the study of the regulation of animal numbers forms about half the subject of ecology, although it has hitherto been almost untouched. If the climatic cause of the fluctuation could be predicted, the position would be better still.

The following suggestions as to the effect of periodic fluctuations in the numbers of animals upon the method of evolution are speculative, but at the same time are mostly self-evident when once thought of; that is, they evidently must be factors affecting the animals. The question of whether they are important factors will have to be decided by further work.

(1) I am assuming here that natural selection must be sometimes effective in changing the race, and the only question is when, how, and how much. (In face of the enormous number of facts that are explained by natural selection as a hypothesis, it is for those who do not believe in it to disprove its truth.) In all the rodents whose periodic overpopulation is ended by epidemics, there must be strong selection of individuals for resistance to the disease, and this does not happen continuously, or even every year, but once every three or four or every eleven years. In the intervals the parasite which is the cause of the disease must also be undergoing severe individual selection for dispersal powers, since the numbers of its host are much reduced. So there is alternate selection of the host and the parasite. We do not know to what extent this selection really changes the race, i.e. whether animals survive on their genotypic merits, but at any rate it seems very probable. Again, there is periodic severe climate, such as the bad winters which occur in England at intervals. There is some evidence that selection really does happen in these years in such a way as to alter the race. The Dormouse (*Muscardinus avellanarius*) hibernates in winter in a nest. After the severe winter of 1860-61 many were found dead in their nests in Essex. The continental race habitually survives the more severe winters there, apparently owing to the fact that it makes a thicker nest and is thus more efficiently insulated (Barrett-Hamilton, 1910). If this is so, we have a case where selection of an instinct has differentiated two races without any accompanying obvious change in structure. In all these cases the factor causing the selection acts at intervals; so that if the climate of the country is becoming progressively worse, the mice in it are not subjected to a minute change in conditions every year, but have the eleven years' accumulated change acting suddenly at the end of that time. Thus the animals are tested by selection for some characters at intervals of eleven years, or of three or four years in the case of the lemming. The subject of natural selection for adaptation to climatic conditions must be very complicated, since there are not only these short periodic pulsations of climate but also the longer ones of hundreds or thousands of

years (cf. Pettersson, 1912; Huntington, 1914), and then the still larger ones of the size of ice-ages.

A further factor in this periodic selection is that while in maximum years there is selection of individuals, e.g. for resistance to disease, ability to escape enemies, ability of the males to secure females in competition with other males, etc., in the minimum years there is selection for resistance to bad climatic conditions, and if the animals are few and scattered, for ability of the males to find their mates, although there will be little competition for them when once found. There will thus be different types of selection at the maximum and the minimum in numbers. If such selection is effective in changing the genotypic constitution of the species, it is obvious that the alternate selection in different directions is an important phenomenon.

In the case of many factors, they are acting on animals more or less all the time, but increase in severity periodically e.g. the attacks of enemies (cf. the arctic fox and ptarmigan). Now it is well known that mass selection does not necessarily select out animals on their genotypic merits, especially when the character on which it is acting is highly modifiable. Thus selection of normal intensity might produce no effect on the hereditary make-up of the species. But if the intensity increases periodically and becomes very great, then selection may begin to discriminate by its severity between the genotypic constitution of individuals.

(2) It is obvious that if natural selection for a particular character were only effective say, once every ten years, there would be no selection in the intervals, and therefore if any new mutation affecting that character were to arise and establish itself in the intervals it would be temporarily indifferent, i.e. neither adaptive or harmful. But, say, five years later, it would be acted on by the periodic selection and might then turn out to be either good or bad, or might remain indifferent. Now it usually is supposed that a new character could hardly ever establish itself or spread in a species without the aid of natural selection. On this basis, characters which were only selected at all every ten years would therefore only be able to arise and spread at all in

one year out of ten. But if we could show a way in which an indifferent mutation, i.e. one which at the moment was neither adaptive or harmful, could arise and spread in the species, without the aid of natural selection, there would be far more material for the periodic selection to act on. There can be little doubt that there are many cases of indifferent characters existing in a species, and what is more forming the characters which distinguish closely allied species. The great problem has always been to explain how such indifferent characters could become established in a population at all often. The only adequate explanation put forward so far is that these characters are a by-product of hereditary factors concerned with adaptive characters; but this does not seem to cover the facts at all completely, although it undoubtedly explains some cases. At first sight it seems very unlikely that any new character could spread or even survive, unless selection were acting in its favour. For instance, in *Gammarus pulex*, the freshwater amphipod, the chances of any one young animal reaching the adult state and breeding are about one in a thousand. It is clear that if the rate of mutation is slow, a new mutation arising in a single animal apparently has an extraordinarily small chance of establishing itself and breeding, much less of spreading in the population, unless selection is acting in its favour. But this difficulty vanishes when we realise that animal populations do not remain stable. The case of Gammarus is a good one. There is a stream near Liverpool, in which *G. pulex* lives, but which dries up periodically, all except some deep ponds near the source. The Gammarus stock in the stream of course is wiped out periodically, and the bare area of several miles of stream is recolonised by the animals from the ponds. Now while this recolonisation is going on, there is practically nothing checking the numbers of the shrimps, and consequently the chance of survival of any individual may be one in two, or even a dead certainty. In other words, the struggle for existence ceases temporarily. If several animals are responsible for starting the new stock, practically all their families will grow up, and any mutation that happened to occur or be contained as a recessive at such a time of spread with no checks, would automatically spread unless it was actually very harmful. This idea does seem to be confirmed by the excessive number of varieties of *G. pulex* in this stream (which are at the moment under experimental analysis). The fluctuation among rabbits presents an exactly similar appearance. There is great abundance followed by almost complete destruction of the rabbits, and then increase to fill up the places that have just been emptied. Any new variation arising at this time would inevitably spread as in the case of Gammarus, and if it was useful would be selected favourably at the next periodic "examination"; if it was absolutely indifferent from the point of view of adaptation, it would remain as a character, and its further history would depend on other considerations; cf. Haldane's striking mathematical analysis of the spread of mutations under the action of natural selection (1924). The difficulty of imagining how a mutation gets a start in a population is removed when the full significance of fluctuations in numbers is realised. The chief question which arises is whether the chance of a new variation cropping up in the small nucleus of individuals that start the new stock is not very small. If the idea put forward here is correct, the method of regulating its numbers is a vital factor in deciding the evolutionary path of a species. It is interesting to note that the beaver, which we have seen to lead a very regular sort of life, with no fluctuation in its numbers, has practically no geographical races, and in this is unlike the mice. This may be a coincidence, or it may be that the beaver has obtained temporary security at the expense of ultimate progress, owing to having now no mechanism for accumulating the "capital" of variations on which natural selection could act.

(3) When rabbits, lemmings, mice, etc., die off through epidemics, there are remarkably few animals left in the district. The example of the musk-rat is not an unusual one. Observers describe the emptiness of the mountain tundras in Norway after a lemming-year has occurred. This has an important bearing in the way mentioned above, in that the new young are able to spread into what is

practically an empty habitat, in a way entirely comparable to the colonising of bare ground by plants; but it must also have an important influence in keeping the specific characters uniform in the population. If the whole population of thousands of individuals arises afresh from a few animals every eleven years, then the genotypic constitution of the species will tend to become comparatively pure. Or, to put the matter another way, every time a minimum in numbers occurs, there is the chance of the less common genes becoming extinct, so that the total number of genes for any one character would tend to become reduced. Hagedoorn (1921) has already pointed out the importance of any fluctuation in the numbers of animals in causing uniformity, but he definitely states that the numbers of all common species remain constant from year to year. The fluctuations to which he refers are the irregular ones such as the colonisation of new empty habitats by a few individuals, or irregular climatic and biological factors. The facts about periodic fluctuations in animals, therefore, merely make his conclusions of wider application. He also suggests that although the numbers of a species remain constant usually (which is, however, not the case), only a certain number of individuals breed each year out of the population which has survived. This would have the same effect as fluctuation in the actual numbers. There is practically no evidence of this, however, but it may sometimes be important. Hagedoorn also tried to prove that genotypic purity was bound to occur in a stable population; but this has been criticised on mathematical grounds, and is probably not the case.

The degree to which a species does remain uniform in characters will depend therefore not only on the factors usually quoted, such as natural selection and crossing, but also on the extent of its periodic fluctuations. This does not contradict the other idea about establishment of new variations, since the latter process may not happen very often. In fact there is in many animals a mechanism by which variation in the population are alternately acquired and weeded out, or kept as indifferent characters, which in turn may become useful at some crisis in the history of the animal at a later date.

(4) These ideas, which follow from the realisation of the existence of fluctuations in the numbers of animals, do help to explain some of the difficulties which arise in studying the method of evolution. The fluctuation in numbers explains (at any rate theoretically and in the animals which do fluctuate) several things; firstly, how by a temporary cessation of the struggle for existence, new mutations which are indifferent (i.e. neither adaptive nor harmful) can occasionally get a footing and spread in the population; secondly, how, in all probability, some characters are selected periodically; thirdly, how the species remains on the whole uniform in composition. A fourth important conclusion follows from the recognition of factors other than selection and crossing causing uniformity. One of the great problems in adaptation is how an animal can have, as it often does, a particular structure or habit, which has only a general adaptive significance. Thus, in the case of certain colour patterns, such as ruptive coloration for protection, there often seems no point in having that one particular pattern rather than another, although the general survival significance is clear enough. It is difficult to see how natural selection could discriminate to such a fine point, so as to eliminate other equally good patterns. The difficulty is explained when we realise that the uniformity caused by fluctuating numbers acts without reference to adaptation. There is, so to speak, an entrance examination by natural selection, which weeds out the worst candidates, but the final selection is by lot.

### 5. Summary.

1. Four main points are dealt with :—

(*a*) The widespread existence of fluctuations in the numbers of animals.

(*b*) The existence, in many birds and mammals, of periodic fluctuations (p.f.).

(*c*) The cause of the latter, which must be some periodic climatic change acting over wide areas.

(*d*) The effects of fluctuations in general, and in particular of the p.f., on the method of evolution and other biological phenomena.

## Periodic Fluctuations in Numbers of Animals

2. A short sketch is given of what is known about short-period climatic cycles (2 to 20 years), and their causes.

3. P.f. of lemmings have an average period of about $3\frac{1}{2}$ years. The maxima in numbers occur synchronously in North America and Europe, and probably all round the arctic regions.

The varying hare in Canada has a period of 10 to 11 years.

5. The only regular periods shown by the animals dealt with are the short one of $3\frac{1}{2}$ years and the longer one of 10 to 11 years. The former is probably more marked in the arctic and the other further south.

6. The sandgrouse p.f. point to the existence of an 11-year climatic cycle in the deserts of Central Asia.

7. The effects of these p.f. on evolution must be very great, although at present problematical; but the following suggestions are made :—

(*a*) Natural selection of some characters must be periodic.

(*b*) There will be different types of natural selection at the maxima and minima of numbers.

(*c*) The struggle for existence, and therefore natural selection, tend to cease temporarily during the rapid expansion in numbers from a minimum, and new mutations have then a chance to get established and spread, i.e. without the aid of natural selection. This might happen only rarely.

(*d*) This would explain the origin and survival of non-adaptive characters in a species.

(*e*) On the other hand periodic reduction in numbers will act as an important factor causing uniformity in the species.

(*f*) The opposing factors (*c*) and (*e*) will vary much in different species, and the problem will require the combined attentions of mathematicians, and of ecologists working on the methods of regulation of the numbers of animals.

(*g*) This mechanical uniformity factor, since it acts independently of natural selection, explains how a particular structure or habit may evolve, when it only has a general adaptive significance.

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