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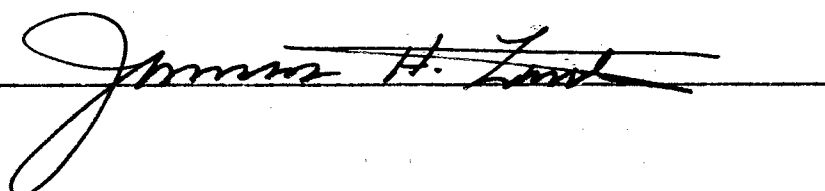Pages in Study: 29   Candidate for Degree of Master of Science

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Scope and Method of Study: The question as to whether or not mammals exhibit population cycles, and if so the cause or causes for the cycles, has been, and still is a controversial one. Much of the literature contains theories and conclusions that have been disproved since the time of publication of the article. In reviewing the literature the faulty accounts were separated out and only that evidence and those theories that have been accepted by the majority of investigators were considered.

Findings and Conclusions: Definite accounts of population cycles have been published for lynx, hare, lemming, various foxes, some voles, and muskrats. There are two distinguished types of cycles shown (1) cycles of about ten years, in the snowshoe hare, muskrat, lynx, and foxes, (2) cycles of about four years, in voles, lemmings, and the carnivores of the arctic.

Postulated causes of mammal population cycles backed up by serious evidence include: a depressing factor brought on by stress, mineral deficiency caused by eradication of plants by high populations, exhaustion of the adreno-pituitary system resulting from increased stresses inherent in a high population plus demands of the reproductive system, and shock disease dependent upon a high density of population and related to the immediate environment. Sunspot activity and mammal cycles have been thought to be correlated, but all evidence is negative for the theory. Disease, parasites, and predators do not appear to be of primary importance for causing decline in prey populations. Population cycles in mammals seem to be caused by a number of factors, all acting together to cause the cyclic fluctuations.

ADVISER'S APPROVAL _____

CYCLES AND THEIR POSTULATED CAUSE

IN MAMMAL POPULATIONS

By

HAROLD W. MCGEHEE

Bachelor of Science
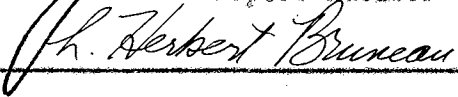
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CYCLES AND THEIR POSTULATED CAUSES

IN MAMMAL POPULATIONS

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PREFACE

The question as to whether or not mammals exhibit population cycles, and if so the cause or causes for the cycles, has been, and still is a controversial one. There has been a great deal of literature published concerning cycles, some of it backed up by valid evidence and some of it nothing more than guess work. To review and evaluate this published material is the purpose of this report.

Before a report can be written a complete review of the vast amount of literature that has been published on cycles in mammal populations must be made. Much of the literature contains conclusions and theories that have been disproved since the time of publication of the article or arcticles. These faulty accounts have been separated out and only that evidence and those theories that have stood up under contiued investigation and shown to have merit have been used in the report.

Indebtedness is acknowledged to Drs. J. H. Zent and L. N. Bruneau for their valuable guidance.

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CHAPTER I

INTRODUCTION

For centuries it has been recognized that some species of animals at times occur in such abundance as to become serious pests, and at other times are so reduced in numbers that they can scarcely be found anywhere. It is only during the last three decades that any really intensive study has been made of the mechanics and causes of these fluctuations. Most of the work has been done in North America; first under the impetus provided by a more widespread interest in hunting game, and second, following an awakening awareness that the behavior of animal populations constitutes a largely unexplored frontier, one which may quite possibly lead to a better understanding of some of the problems involving human populations and to methods for solving them.

Of all the species for which there is an adequate record, the beaver is the only one known not to fluctuate. There are doubtful cases of fluctuations that resemble those of cyclic species, but are not yet shown to be cyclic. Definite accounts are published only for lynx, hare, lemming, various foxes, some voles and muskrats. There are two distinguished types of cycles in mammal populations as follows: (1) cycles of about ten years, in the snowshoe hare, muskrat, lynx and foxes, (2) cycles of about four years, in voles and lemmings and also in carnivores of the arctic.

There have been many causes postulated for cycles in mammal popu-

lations. Some of these have been thoroughly disproved and are not included in this paper. The ones that are backed up by serious evidence include: a depressing factor brought on by stress, mineral deficiency caused by the eradication of plants by high populations, exhaustion of the adreno-pituitary system resulting from increased stresses inherent in a high population plus demands of the reproductive system, and shock disease dependent upon a high density of population and related to the immediate environment. Sunspot activity and mammal cycles have been thought to be correlated, but all the present evidence is negative for the theory. Diseases, parasites, and predators do not appear to be of primary importance in regulating mammal cycles, but they do show secondary importance for causing decline in prey populations.

The belief of most investigators is that cycles in mammal populations are not caused by one major factor acting alone, but are brought about by the accumulated effect of several factors, each contributing to the over-all cause of the cycles.

CHAPTER II

CHARACTER OF POPULATION CYCLES

There are three general types of population fluctuations to be noted: the flat, the irruptive, and the cyclic. The flat type is undergone by the great majority of animals; the minor, year to year variations in numbers of individuals may be due to availability of food, condition of cover and breeding conditions. Such variations are localized and entirely irregular; the total number of individuals of the species involved tends to remain relatively constant over an indefinite period of time.

The irruptive type of fluctuation is characterized by the species exhibiting the flat type of variation for a seemingly indefinite period, then in the short span of a year or two, it increases nearly to plague proportions. Almost immediately thereafter there begins a comparable decrease in numbers, the population dropping to normal or slightly below.

The cyclic type of population behavior, and the one that will be reviewed in this paper, is characterized by a rhythmic change in the numbers of individuals; the cyclic waves in length from three or four years to ten or eleven years. The rise is typically gradual, extending over approximately two-thirds or three-fourths of the time required to complete the cycle. The subsequent die-off occurs more rapidly, and usually results in a loss of about seventy-five percent of the peak or

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maximum population (Elton, 1942).

There are two important aspects of mammalian cycles to be considered next: (1) the fixed cycle length for each general size of mammal, and (2) the difference in degree of cycling between the sub-arctic and more temperate and tropical climates. What follows applies primarily to rodents, since predators merely reflect the cycles of their food supply. For example, the foxes of Ungava closely follow the vole and lemming cycles upon which they depend for food (Elton, 1942).

Voles, mice, and similar mammals have an approximately four year cycle (Hamilton, 1937; Elton, 1942; Clarke, 1949). Larger mammals, such as hares, rabbits, and muskrats, have about a ten year cycle (Elton, 1942; Clarke, 1949; Green et al., 1938a), while still larger mammals have still a longer cycle (Clarke, 1949). The first fact which strikes one is the apparent relationship between cycle length and body size, but this in itself does not seem to be the answer. It seems likely that the short period of sexual immaturity, the short gestation period, and the large litter sizes of the smaller mammals are the prime factors in the short cycle. These factors lead to a lower reproductive potential in the medium-sized mammals, for example, snowshoe hares require at least a year to reach sexual maturity and have a gestation period of 38 days (Aldous, 1937) as apposed to 25 days and 21 days respectively, for the meadow vole Microtus (Hamilton, 1941). The larger animals, such as caribou, probably have an even longer cycle correlated with gestation period of 7-8 months, and reach sexual maturity at 1.5 years (Asdell, 1946). In other words, it seems highly probable that the cycle length is a function of the reproductive potential of the given animal. Those with the highest reproductive capacity build most rapidly

to a population peak in excess of the carrying capacity of the environment. It is notable that the most prolific animals of their respective size groups (e.g. meadow voles and snowshoe hares) are the most prominently cyclic. Starting with a population low, there is a period of relatively heavy predator pressure on a minimal population (Elton, 1942). At this time the excess of the births over the death rate will be very small, but must exist for a population increase to occur, and it is the excess which is of primary interest. Taking only this excess, it is understandable that this segment of the population will increase exponentially in relation to its reproductive potential. In the highly prolific meadow vole with a short period of immaturity and short gestation period, an average litter size of 5.5 (Asdell, 1946), and capable of having up to 17 litters annually (Bailey, 1924), it can be seen that rapid increases to enormous levels are possible, and do occur. An additional factor, pointed out by Hamilton (1937), is the progressively increasing chances of immediate post-parturient mating with a resulting increased number of litters per year as the population rises and contracts between sexes increase. A further well-known fact tending to accelerate the rate of reproduction is the increase in average litter size for about the first half-dozen litters. In an increasing population the average age is similarly increasing, which means that more maximum-sized litters are born, as well as more females reaching reproductive maturity. Since the potential reproductive capacity of any species, as well as the death rate, is relatively fixed, the cycle length will be related directly to the time it takes the population excess over the death-rate to peak to a point beyond carrying capacity of the environment, and hence highly stressed conditions (Odum, 1953).

It can be seen that in this fashion the lower the reproductive capacity of the species, the longer will be its cycle. Environment in this discussion is used in the broadest sense, including predators, interspecific relations, and all other factors. Exceptionally severe or favorable environmental factors could possibly shorten or lengthen the cycle a year or so, depending upon whether operative early or late in the cycle. If extremely unfavorable conditions were brought to bear on a population at its ebb, it is conceivable that peak attainment could be delayed a year. Conversely, if this occurred when the population was high, but not at its peak, a relative peak would be caused with a resultant die-off.

The species believed to experience cyclic population changes seem to be almost entirely confined to the Northern Hemisphere, although Hudson (1892) mentions cycles in the Southern Hemisphere rodents.

By and large, the number of species exhibiting cyclic behavior increases as one proceeds northward in the Northern Hemisphere. This is true throughout the temperate regions, and in the arctic, where there are markedly fewer species, the fluctuations reach their greatest extent, both in spread and violence. Animals with plenty of space and a high biotic potential have cycles. The same species, where cramped and restricted, and at the limit of their range cease to be cyclic (Elton, 1942).

CHAPTER III

EVIDENCE OF POPULATION CYCLES IN MAMMALS

The literature giving evidence of population cycles in mammals is well summarized by Mac Lulich (1937), Elton (1942), Dymond (1947), Siivonen (1948), and Clarke (1949). These authors tend to divide the animals which participate in cycles into two classes: prey animals such as mice, rabbits, and lemmings; and predators such as lynx and fox. The main assumption in the literature is that the prey cycle is the basic one and that the predator cycle merely follows the prey one.

The cycles of the mammalian predators are well documented through the fur sales of the Hudson Bay Company, analyzed by Elton (1942) and Elton and Nicholson (1942 a,b). There is a 4-year cycle in the tundra, found in the arctic fox which preys on lemmings, a 4-year cycle in the subarctic open forest to the south, found in the red fox and the martin, which there prey primarily on voles, and a 10-year cycle in the northern forest region, found in the lynx and other mammals which prey primarily on the snowshoe hare and is less clear in the red fox and other species, which turn rather freely to other prey when hares are scarce (Lack, 1954).

Marten and red fox have a 4-year cycle in northern Labrador and Hudson Strait, where they prey chiefly on voles, and a 10-year cycle in the forest belt farther south, where they prey mainly on the snowshoe hare (Elton, 1942). Also on the Vancouver Island, the marten eats chiefly mice and squirrels and has fluctuated independently of the

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well-marked 10-year cycle on the adjacent mainland of British Columbia
(Cowan, 1938). Again, the arctic fox has a 4-year cycle in those parts
of Greenland where lemmings are present, but fluctuates irregularly
where lemmings are absent and it eats mainly ptarmigan and arctic hare
(Braestrup, 1941).

During the rodent declines the carnivores are often found weak or
starving and food shortage is clearly the main cause of their death.
Disease has been reported at times, particularly among foxes (Elton,
1942).

The catches of red fox in Ontario show a regular cycle when summed
over a wide area, but fluctuate erratically at individual collecting
posts (Cross, 1940). Hence there are local variations. There are also
regional differences, since in the lynx the peak of the cycle may differ
by from 2 to 4 years in different parts of Canada; but the degree of
divergence does not increase the time, and different areas tend to get
back into step (Elton and Nicholson, 1942a). Such local and regional
variations seem to be characteristic of cyclic animals in general. The
tendency for the predator cycles in different regions to get back into
step with each other may be due to a similar tendency in their rodent
prey, but it is almost certainly assisted by emigration (Lack, 1954).
Thus the lynx sometimes emigrates in great numbers, as in 1916-17
following the snowshoe hare peak of 1914-15 (Hewitt, 1921). Movements
also occur in the red fox Butler, 1951) and in the arctic fox, which
may even cross from Canada to Greenland over the ice (Braestrup, 1941).

The evidence given above should be enough to show that cycles of
the predators depend basically on those of the rodents. The under-
lying causes of the rodent cycles are much more obscure. The main

feature of these cycles have been summarized by Elton (1942), and Chitty (1950a). First, the successive peaks come at extremely regular intervals. Secondly, the peaks may be up to 2-years out of step, and in the snowshoe hare up to 5 years out of step, which are the greatest possible discrepencies in a 4-year and a 10-year cycle respectively. There was a peak for the snowshoe hare somewhere in Canada every year between 1939 and 1946 (Chitty, 1950b). Thirdly, the size of the successive peaks may differ greatly, as is well shown for the lynx (Elton and Nicholson, 1942a). Fourthly, the peaks are usually much larger in the north than the south of the range, a point which holds for all the cyclic animals in which it has been examined (Cowan, 1938; Dymond, 1947).

CHAPTER IV

POSTULATED CAUSES OF POPULATION CYCLES IN MAMMALS

There seems to be two main types of explanations that have been put
forward to explain the mammal cycles, one envolving an extrinsic cause,
usually climatic, and the other an intrinsic cause, usually a predator-
prey interaction. Advocates of the first type of cause have usually
laid main emphasis on the increase in the reproductive rate leading to
population peaks, and advocates of the second type on the heavy mor-
tality in the periodic crashes. As rightly pointed out by Dymond (1947),
it is the periodic declines, not the increases, which require expla-
nation, since mammals can increase extremely rapidly when unchecked.

Many postulated causes of population cycles in mammals have been
put forward, some of these have been thoroughly disproved and others
are not supported by enough serious evidence to warrent discussion at
the present time. The sunspot theory, which had been held by some
investigators to be the cause of cycles in mammals, has been satis -
factorly disproved by Mac Lulich (1957), but will be summarized briefly
in this paper to show the thinking behind the idea.

Each of the postulated causes for population cycles in mammals will
be taken up separately, but some of the evidence and examples used to
explain the principles of each may tend to be intergrades in explaining
all of them. The reason for this is that there is no evidence which
points to one and only one isolated cause of the cycles, but instead all
of the causes postulated tend to operate together to cause population

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cycles.

Sunspots and Cycles in Mammals

Sunspot cycles have been recognized for a long time, and attempts
have been made, at one time or another, to correlate with them almost
every phase of climatic variation, human activity and plant and lower
animal behavior. At first thought, of course, it seems somewhat
obsured that "spots" on the sun, about 93 million miles distant from the
earth, could have any appreciable effect upon, for instance, the snow-
shoe hare in North America. However, the sunspots undergo a cycle
increase and decrease with a periodicity of eleven years. Perhaps this
similarity between animal cycles and sunspot cycles is merely a coinci-
dence, and perhaps not. It will be noted that species affected by
cyclic fluctuations may be divided into two groups: those that obtain
their food directly from plants and those that feed on these plant-
eaters. Now, if there is a drastic reduction in the numbers of a plant-
eating (herbivorous) species, it is inevitable that there also be a
comparable reduction in the numbers of meat-eaters (carnivorous) feeding
upon them. The latter will starve simply because there is not enough
prey to go around. It seems logical, then to look to the herbivores ___
the rodents, the hares and grouse ___ for an explanation of the causes
of cycles inasmuch as they constitute the first step in the "food chain".

During the maximum of the sunspot cycle, i.e., when the surface of
the sun bears the greatest number of "spots", the proportion of ultra-
violet rays in the sunlight reaching the earth is higher than at other
times. It is known that a high proportion of ultra-violet light has a
retarding effect on plant growth. It has also been ascertained that

during the years of sunspot maxima, more inclement weather occurs than
at other times. With less food available, even by a little (due to
retarded plant growth) and with less favorable weather conditions pre-
vailing at these times, it appears reasonable to assume that herbivores,
especially those feeding on tender green portions of the plants, would
suffer, both through direct starvation and, less obviously, through a
general weakening of the population because of malnutrition. Poorly-fed
individuals succumb more readily to the effects of parasites and disease
than do well-fed ones; hence a population, having by a lowered food
supply and an increasing vulnerability to disease, is inevitably reduced.
This reduction is, then, one of the factors which act to prevent unre-
strained increase in species which otherwise might conceivably increase
indefinitely.

This theory is subject to many criticisms. In the first place, it
is apparent from the records, that the cycle does not act simultaneously
throughout a species, even in a relatively small area. Cross (1940),
working in Ontario, and analyzing the Hudson's Bay Company reports of
1916 through 1938 in that province, has shown that the red fox, although
experiencing local changes in numbers resulting from changing local
conditions. On the basis of his results, Cross states that "... fluctu-
ations in the number of the fox in Ontario are definitely not correlated
with sunspots ..." The sunspot theory was given another set back by the
work of Mac Lulich (1937) who, after studing the records for the snow-
shoe hare and Canada lynx, concluded that the fluctuations of neither
are correlated with sunspots.

The Influence of Food on Mammal Cycles

Braestrup (1940) suggested that a decline in the quality of food as a result of a regular climatic change may cause hare cycles, but subsequent study has not borne out the climatic cycles. He also expressed the belief that nutritional problems may result from over utilization of the food species long before any general over utilization of the food supply is apparent. Grange (1949) proposed that cycles were the result of the interreaction between herbivorous mammals and their food supply. Such a simple cycle assumes that the animals' populations build up until they consume all of the food, then die off and rebuild again after the food supply has recovered. Studies of lemming populations at Point Barrow, reported by Thompson (1955), suggest a cycle almost that simple. He reports that almost all vegetation was consumed at the peak of the three to four-year cycle. Although Thompson concluded that the cycle was due to a combination of predation and food and cover depletion, it is quite apparent that some cycle would have resulted even if the lemmings taken by predators were already doomed to starve. An indication that rabbits may also respond to such a simple starvation cycle is found in reports that they sometimes severely damage their winter food plants during peak years (Bailey, 1946). However, such examples of direct starvation limiting herbivore populations are relatively uncommon in nature, malnutrition, not starvation, usually sets the population limits, in the opinion of the author. Most animals resort to so-called "stuffing foods" (Leopold, 1933) rather than succumb to direct starvation. Actually, the rabbits mentioned above which were damaging their ranges, probably were consuming foods that were below their minimum nutritional requirements.

Most living things have a reproductive capacity that keeps their population at environmental capacity, and the most important single component of the environment is food. This is borne out by Lack (1954), who concludes that many bird species are "limited in numbers by their food supply." Leopold (1955) gives further support to this conclusion when he states that food is the "all-important" regulator of deer numbers.

Herbivores consume first their sustaining food plants; when these are gone, they turn to marginal food plants, and if they in turn are all used, they must resort to submarginal species that are below their minimum requirements. During the winter when the food supply is at its lowest level most northern herbivorous populations are most likely to be forced to utilize foods that are nutritionally close to the minimum necessary to maintain health or sustain life. The pressure of reproduction tends to keep the population at this malnutrition threshold. The animals that are forced below this threshold do not immediately die, but generally weakened, are less able to protect themselves. They are more susceptible to the attacks of parasites and disease, and they show a lower rate of reproductive survival (Allen, 1954). These are all symptoms that are commonly found in a cyclic population in its declining phase. For example, Green's work (1939) on "shock disease" of rabbits suggests a nutritional deficiency as the primary cause. Mac Lulich (1937) showed that several diseases may be involved in the decline of some cyclic species. Low reproduction, or low survival of young, has been found in most studies of the decline of cyclic animals (Siivonen, 1952; Lack, 1954). These correlations are circumstantial evidence that cyclic decline is nutritional, probably associated with either a decline

in the quantity or quality of the food supply.

Koskimies (1955) suggests that cyclic losses of northern herbivores are biologically necessary to protect the slow-growing northern vegetation from over-utilization. It seems that the cycles must have some survival value, or the animals would have developed adaptations to overcome them. Apparently the animals and their food plants evolved together and those that over-utilized and destroyed their food supply also destroyed themselves (Allee, et al., 1949). For example, if a squirrel were evolved that could thrive on any or all twigs and buds of coniferous trees, there would be little to halt its increase until all conifers were killed, because there is no way in which a tree could escape from a horde of hungry squirrels. However, if there were several species of coniferous food plants present, each of a different nutritional value, the squirrels would undoubtedly over-utilize and possibly kill the ones of high food value, but trees of marginal quality could probably survive. They would be protected if only a part of the foliage of an individual tree were nutritionally adequate to serve as squirrel food, or if only a few individual members of a plant species were vigorous and rich enough to sustain squirrels. These are all possible methods by which marginal plants may retreat below the nutritional minimum required by animals. It would seem that all plants must develop some method of escape from total utilization by herbivorous animals with the result that many have evolved near to this malnutritional threhold. Those animals that must depend upon these plants of lowered nutritional value must find a new source of food or decline in numbers or possibly disappear from Nature's picture.

Exhaustion of the Adreno-Pituitary System as a Cause of Mammal Cycles

Although it may seem reversed, this discussion will start at the end of the cycle, because the die-off is its most startling phenomena as well as one of the major problems to be explained. This crash has been sufficiently described by Elton (1942) to make unnecessary any further description of its general aspects here. Suffice it to say that the crash occurs following a peak in the population, and terminates a cycle of increasing abundance. More detailed accounts of several investigations on crashes are given below to lend evidence for conclusions drawn later.

In 1909 Piper described an outbreak and subsequent die-off of meadow voles (Microtus montanus) in Nevada. The peak was reached in the winter of 1907-08, and followed by the crash from January to March of 1908. All attempts to relate the die-off to a causitive organism failed.

Elton, Ford, Baker, and Gardner (1931) intensively investigated a predicted crash in Apodemus sylvaticus in late winter and early spring, and were wholly unable to demonstrate any causitive organism. No recognizable pathological lesions were demonstrated. These authors did not definitely rule out the possibility of a virus infection, but they believed it extremely unlikely on the basis of negative lesions findings. Their conclusions were that "some obscure biochemical or physiological condition of the mouse population caused the animals to die in captivity, after being brought in from the wild, with the most unusual regularity and rapidity." Animals brought into the laboratory died within a day or so under identical conditions to those previously

kept for three weeks or more. They stated that something was at work in the mouse population that was able, either without shock or stress of the mice being trapped and brought into captivity, or with the aid of these factors, to destroy the mice extremely quickly, and before any important lesions had developed. They assume that the mice were weakened by some factor the investigation did not reveal.

Findlay and Middleton (1934) definitely ruled out bacteria and viruses as causitive agents during a die-off of Microtus agrestis. Preceding death in these animals there was a lethargic period followed by a period of convulsive activity. The authors stated that the mice exhibited head retraction, circular movements, hunching of the back and frequently paralysis of the hind limbs associated with periodic convulsive movements. They found that sometime sudden death occurred during the convulsions, but that more commonly the voles passed into a comatose condition, followed after a short period by death. Cysts of Toxoplasma were found in the brains of 19 out of 34 voles in sufficiently good condition for careful examination. This organism is quite widespread normally, and occurred here in over half of the animals that died. It hardly seems probable in view of the authors' findings that Toxoplasma can seriously be considered as the prime cause of decimation in the voles. The salient fact is that here again are animals dying without demonstrable cause.

Hamilton (1937) studied Microtus pennsylvanicus population in the region of Ithica, New York, from 1924 to 1936, with intensive work from the spring of 1933 to the fall of 1936. Over 4,000 animals were examined during this time. A population high was recorded in the winter of 1935 - 36, and was followed by a period of marked mortality from

March to June 1936. Hamilton assumed that disease was the paramount factor reducing the spring population, and points out that epidemiologically ideal conditions existed for the spread of disease during a population peak. Animals of all ages were affected. The symptoms found in the dying mice were sluggishness, ruffled fur, and lethargy. After incipient drowsiness, a characteristic spasmodic twitching of the neck and shoulders occurred with the animals falling on their side. The animals finally died in convulsions after preliminary extensions of the hind legs. These symptoms are remarkably like those described by Findlay and Middleton above. Laboratory examinations of mice dying in convulsions revealed no pathological lesions, nor could causitive organisms be demonstrated. Again a filterable virus could not be definitely ruled out. Brain examinations were completely negative. External parasites were extremely abundant, but Elton (1942) has shown that this is the result of the increased age of the animals which have wintered over from the preceding fall. Once again the deaths are unexplained.

Green and his co-workers (1938a, 1938b, 1939), during an intensive study of the periodic die-off in snowshoe hares in Minnesota, were able to demonstrate that a very small number of deaths could be attributed to infectious disease. The majority of animals exhibited a characteristic syndrome which the authors have termed "shock disease". This syndrome was characterized primarily by fatty degeneration and atrophy of the liver with a coincident striking decrease in liver glucogen and hypoglycemia proceding death. Petechial or ecchymotic brain hemorrhages and congestion and hemorrhage of the adrenals, thyroid, and kidneys were frequent findings in a smaller number of animals. The hares characteristically died in convulsive seizures with sudden onset, running move-

ments, hind-leg extensions, retraction of the head and neck, and sudden leaps with clonic seizures upon alighting. Other animals were typically lethargic and comatose. Some showed a combination of these two states. The similarity of these symptoms, and those of the mice above, to those of hypoglycemic convulsions is notable. Best and Taylor (1939) give the following description and symptoms of hypoglycemia produced by any means:

"The signs in the rabbit are hyperexcitability and desire for food. The excitability becomes greater, and mild and then severe, convulsions are exhibited. The head is retracted and hind limbs extended in the intervals between convulsive seizure. Coma is frequent. The animals may exhibit rigor mortis immediately after death. The signs in dogs are quite similar. Mice, in some instances, may become comatose without exhibiting convulsions."

Green et al. (1939) emphasized the inability of the animals to withstand any undue exertion or stress which would leave normal animals unaffected. These findings were demonstrated equally in all hares older than seven weeks, and this is important, since it shows that factors which induce shock disease exert sufficient influence to produce deaths in both young and old animals in nature. The population studied reached its peak in 1933, and the decline was continuous to 1937, with the greatest die-off being in the fall and winter of 1935. Similar observations reached were that shock disease is primarily responsible for decimation of snowshoe hares, that local conditions were attributable, and that severe upsets in carbohydrate metabolism were the primary effect on the hares.

Throughout these various investigations there is a remarkable consistency in the findings, regardless of the species. With possible exception of Findlay and Middleton's Toxoplasma infections no pathogenic organisms could be demonstrated. The onset of symptoms, termi-

nating in convulsions, shows a similar pattern in every case, and all
would appear to be hypoglycemic in nature. All authors pointed to the
increased susceptibility to stress. It seems, then, that what is being
dealt with here is a phenomenon common to all of the animals, and that
Green and Larsen (1938a) have adequately described its pathology and
physiology. Universally these die-offs follow a population peak, occur
primarily in the late winter and early spring, and involve severe meta-
bolic disturbances coincident with markedly decreased resistance to
stress.

In searching for a common cause for these changes it seems that
Selye's adaptation syndrome (1946, 1947(provides an answer to the
problem. In other words the symptoms of adrenal exhaustion on a popu-
lation-wide basis are being dealt with here. Selye (1946) has sug-
gested that Green's shock disease in snowshoe hares resembles a disease
of adaptation. The adaptation syndrome is the sum of the non-specific
physiological and morphological responses to stress other than the
specific adaptive reactions, such as serologic reactions to specific
antigens. Selye has divided these into (1) shock, (2) counter-shock
(these two combined are the "alarm reaction"), (3) resistance, and
(4) exhaustion phase (Selye, 1947), like those of the alarm reaction,
are hypoglycemia, involution of lymphoid tissue, adrenal cortical
hypertrophy, decreased liver glycogen, diminished fat content of the
adipose tissue, lipid deposition in the liver, reversal of the albumen/
globulin ratio, decrease in blood chlorides, rise in blood potassium,
and a marked decrease of the ascorbic acid, ketosteriod, and plasmal
granule content of the adrenal cortex. Frequently during the stage of

exhaustion, the adrenal cortex is found to be hemorrhagic. Often the liver only shows signs of cloudy swelling and decrease in size, but may however, show more intensive atrophy and degeneration changes. These liver changes may be augmented by muscular exercise (Selye, 1939b).

In listing the changes during the exhaustion, or alarm reaction, phase of the adaptation syndrome the findings in animals during the periodic die-off have practically been repeated. Green and Larson (1938a) clearly showed that the convulsions in hares did not occur until the liver glycogen dropped below 0.2 percent, demonstrating that they were caused by a progressive fall in the glucose reserves. experimentally they were able to stop or alleviate the convulsions temporarily by intravenous glucose injections, definitely affirming that the convulsions were hypoglycemic in nature. Epinephrine injections were ineffective. It seems more than likely that in most die-offs in mammals a manifestation of the adaptation syndrome with the terminal convulsions precipitated in many cases by some sudden stress, such as fear, captivity or exertion is being dealt with.

The adrenal response to stress is stimulated by the secretion of adrenocorticotrophic hormone from the anterior pituitary. The mechanism by which the pituitary is stimulated is as yet unknown, but may be brought about by the release of adrenalin (Michael, 1949). As a result of demands on the pituitary of greater life-sustaining importance in response to stress, there is a shift to this function from gonad (Selye, 1939a) and growth (Selye, 1936) stimulating functions, so the growth slows or ceases and the gonads may become atrophic or at least diminished in functional activity. The importance of this factor will

be discussed below. Also of significance is that, when the adaptation syndrome is elicited to one stress, the animal becomes more susceptible to other stresses (Selye, 1947). Fasting (Selye, 1946) and muscular exertion (Selye, 1939b) markedly increase the susceptibility of mammals to alarming stimuli, and may augment the changes which have already taken place. This is especially true of the hypoglycemic phase, and it is probably these factors which determine the final outcome in the form of hypoglycemic convulsions.

The adaptation syndrome may be elicited by a wide variety of alarming stimuli: environmental changes, pregnancy (Sayers and Sayers, 1949), toxic chemicals, bacterial infections (Selye, 1946), fear, rage, emotional upsets (Selye, 1941), cold, muscular exertion, and a great many other (Selye, 1946).

Assuming the die-off is due to a manifestation of the adaptation syndrome, an investigation of the stresses which are at work to produce this effect on a population-wide basis in mammals must be made.

In all the studies so far recorded, the die-off has been in the winter or early spring following a population peak the preceding autumn. Hence there is an extremely high population coming into a period of relative food scarcity, cold and other severe climatic stresses with their attendant sequelae. Along with the attainment of higher population levels, animals are progressively crowded into less and less favorable environments from an originally highly favorable nucleus (Elton, 1942). This means less favorable foods, less good cover, and often unfavorable water supply, and other factors of submarginal living. In all probability every population peak in the wild

exceeds the normal carrying capacity of the environment for that and
other species, in particular during the succeeding winter. Under these
conditions the following stresses would be expected: (1) food scarcity,
(2) lack of proper cover, (3) increased muscular exertion resulting from
longer food forage trips, (4) fights with other individuals (Calhoun,
1949), (5) increased exposure to cold from longer forage trips and
inadequate cover, (6) fighting resulting from territorial encroachment
(Burt, 1940), (7) utilization of inadequate foods, (8) increased ex-
posure to predators due to lack of cover as well as migration of preda-
tors into areas of abundant food supply in the form of a peak population,
and (9) nutritional deficiencies. In summary nearly all emotional nu-
tritional, exertional, and climatic stresses are augmented and operable
upon the entire population. It is of interest to note that this would
impose similar stresses upon animals of all ages, agreeing well with
Green and Larson's findings in hares (1938a and 1939b) in which all
animals over seven weeks of age were involved.

The population at hand is under highly stressed conditions and un-
doubtedly taxing its adreno-pituitary system to the maximum. At this
time*e., in early winter, the day length begins to increase and stimu-
late the pituitary in most animals to secrete gonadtrophic hormones
with resultant gonad development prior to the breeding season. That
daily light stimulates the gonads via the pituitary has been shown for
the snowshoe hare (Lyman, 1941), meadow vole (Baker and Ranson, 1932),
white-footed mouse (Whitaker, 1940), and mink (Hansson, 1947). In
some mammals light has no effect upon the gonad development, but a
period of low temperatures may augment the reproductive activity
(Whitaker, 1940). In any event in all mammals with a spring breeding

season there is a factor placing increased demands on the pituitary at a time when it is already maximally stimulated to produce adreno-cortictrophic hormone in response to stress. That the gonadotrophic function is stimulated in spite of adrenal demands is evident from the fact that the breeding season with production of young does ensue. The argument might be afforded that in some mammals the males are primarily affected by light, but this may be answered by pregnancy demands in the female (Sayers and Sayers, 1949), and growth demands in the young (Selye and Collip, 1936). It has already been shown that the pituitary cannot simultaneously respond maximally to increased demands of all types, but that one type must succumb to another. If, then, the pituitary is under maximum demand as a result of the already-listed stresses and a direct stimulus, in the form of light or low temperature, causes stimulation of gonadotrophic activity, it stands to reason that this latter must occur at the expense of the adrenotrophic activity. Hence at a time when stresses are maximal, there is a sudden increased pituitary load, and animals begin to succumb with symptoms of exhaustion of the adreno-pituitary mechansim and the periodic decimation is in full swing. All of the animals succumbing at more or less the same time is a function of the high population with its inherent stresses.

The time it takes an animal to succumb depends upon the severity and duration of the applied stress. Thus, in a population which reaches a peak in a brief time, the accompaning stresses would be more acutely developed and their application more intense, resulting in a more sudden and pronounced population death. When a population develops

more slowly, the stresses increase at a slower rate, and are applied more gradually which tend to attenuate the final collapse (Sayers and Sayers, 1949).

None of the foegoing theories for the cause of mammal population cycles has been tested under completely natural conditions. The theories have been postulated from limited field observations, which could not be controlled. More study and investigation needs to be done in this area of population fluctuation. The investigator must take every element of nature into consideration. His observation must cover a length of time and a large enough land area to give significant results. These two factors impose problems that will require the combined efforts of many investigators to overcome. The University of Alaska is carrying on a study of the snowshoe hare-lynx cycle which will be done over a lengthy period of time and cover part of Alaska and the Yukon. It is hoped that information gotten from this study will answer the question for the cause of cyclic fluctuations in animal populations.

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