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A STUDY OF MERRIAM'S TEMPERATURE LAWS*

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In 1894, Dr. C. Hart Merriam, of the United States Bureau of Biological Survey, formulated laws of temperature control for the northward and southward distribution of terrestrial animals and plants. At the time that these laws were formulated, they were, undoubtedly, the best statement of the known effect of temperature on limiting distribution. Much work of an ecological nature has since been done, however, and a reëxamination of these laws is needed.

Statement of Temperature Laws

General Considerations. Dr. Merriam was concerned only with the factors of climate which are effective in limiting the distribution of plants and animals during the season of growth and reproduction, which is the open or summer season. He assumed that this season is the only part of the yearly cycle in which temperature exerts a limiting effect upon the distribution of plants and animals, as at other seasons sensitive organisms either become dormant, go into hibernation, or migrate.

Largely on the basis of previous work in the field, Merriam assumed that temperature is by far the most important factor limiting the northward and southward distribution of organisms. He then endeavored to determine which phase of temperature was the critical one by ascertaining what isotherms, when plotted on a large scale map of North America, most nearly agreed with the boundaries of his biotic units, the "life zones", then also in the formative period. The life zones represented unit areas of distribution, each characterized by possessing peculiar genera of animals and plants. If certain isotherms agreed with the boundaries of the life zones, then those isotherms, he argued, must represent the true factor of temperature which controlled the distributional limits of the animals and plants contained therein.

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First Temperature Law. After trying and discarding the use of mean temperature for the reproductive period, use was made of the century-old idea of summation of temperatures. This idea is based upon the belief "that the same stage of vegetation is attained in any year when the sum of mean daily temperatures reaches the same value". A method of summing mean daily temperatures was worked out, and temperature summations were determined for a large number of stations scattered across the continent. When lines (isotherms) were drawn connecting localities with equal sums of temperature, these lines coincided satisfactorily with the northern boundaries of the life zones. He therefore formulated his first temperature law, "*Animals and plants are restricted in northward distribution by the total quantity of heat during the season of growth and reproduction*".

Second Temperature Law. Although these isotherms, so drawn, appeared to agree fairly well with the northern limits of distribution of plants and animals in the life zones, they did not coincide so closely with the southern limits of more northerly forms, notably near the Pacific coast. Wishing to determine the effective phase of temperature which limits the southward distribution of animals and plants, Merriam next plotted the mean daily temperature of an arbitrary period of six weeks during the hottest part of the summer. Isotherms formed from these data agreed with the southern boundaries of the life zones. This led to the formulation of the second temperature law, "*Animals and plants are restricted in southward distribution by the mean temperature of a brief period covering the hottest part of the year*".

Table of Zone Temperatures. Included in his paper is a table giving the critical temperatures which are supposed to limit the northward and southward distribution of organisms. For instance, the northern limit of the Transition Life Zone is determined by a sum total of mean daily temperatures amounting to approximately 10,000° F., the Upper Austral Zone by 11,500° F., the Lower Austral Zone by 18,000° F., and the Tropical Zone by 26,000° F. The southern limit of the Arctic Zone is determined, he supposed, by a normal mean temperature of 50° F. during the six hottest consecutive weeks, the Hudsonian Zone by 57.2° F., the Canadian Zone by 64.4° F., the Transition Zone by 71.6° F., and the Upper Austral Zone by 78.8° F.

Importance of Humidity. Three of the life zones were later divided at about the 100th meridian into eastern and western portions. This was based largely upon a very noticeable difference in humidity.

The east and west divisions are, however, of subordinate rank compared with the zonation north and south.

Acceptance of Laws. These temperature laws were accepted by some biologists, particularly by ornithologists and mammalogists, but not so generally by other zoologists nor by botanists.

The First Temperature Law

It is necessary to consider each temperature law separately, since they are quite different, and criticisms applied to one do not necessarily apply to the other. The first temperature law assumes that summed daily temperatures during the reproductive season control northward distribution.

Season of Temperature Effectiveness. The reproductive and growing season is not, as Merriam supposed, the only time when temperature may be effective in controlling the distribution of animals and plants. Even though some of those forms which do not migrate may become dormant in winter, they are still not insensitive to extreme climatic conditions.

Shreve (1914) studied the relation of winter temperatures to the vertical distribution of vegetation in Arizona and found that "the greatest number of consecutive hours of freezing temperature is the factor most closely corresponding in its distribution, with the limitation of the species concerned". Experimental work with succulent species showed that those which have the lowest vertical limit of distribution were unable to resist freezing over 19 to 22 hours in duration. According to Salmon (1917), the isotherm of 10° F. for the daily minimum temperature of January and February coincides, in general, with the boundary of winter wheat culture in the United States. Northern evergreen trees resist winter-killing by increasing the osmotic pressure and water-retaining capacities of their leaves (Gail, 1926). Some plants are capable of initiating hardening processes to enable them to withstand low temperatures, while others are not (Rosa, 1921).

Hardening, to resist low winter temperatures, occurs also in some species of insects (Payne, 1926). This enables certain species to survive in regions where others, lacking this capacity, can not do so. Sanderson (1908) made a particular study of the influence of winter temperature in controlling the northward distribution of insects. He found that several species are absent from regions where the summation of temperatures during the summer is amply sufficient to allow their reproduction, but where minimum winter temperatures do not permit their survival, even though they are in hibernation.

With birds that migrate south for passing the winter, temperature is undoubtedly of significance in limiting their breeding range only during the open season. However, the wintering range of these birds may often be influenced as much by temperature as is the breeding range and in a similar manner (as in the case of *Troglodytes aedon aedon*), so that temperature is effective, as far as the birds are concerned, at all seasons of the year. Likewise, with birds and mammals which have never acquired the habit of migration but are permanent residents in a region, low temperatures of winter are of utmost importance and undoubtedly exert at that time as much or more influence in determining the distributional limits of the species than they do in the summer. These points are strongly substantiated in a paper which we have ready for publication but unable to include here (Kendeigh, Ms.).

In temperate regions, seasonal changes in the aspects of biotic communities is one of the most striking of ecological phenomena. Nearly all animals and plants undergo differences in behavior and physiology as the winter season comes on. This may be merely an increase in the resistance to low temperatures which occurs in evergreen trees, cold-blooded organisms, and in those birds and mammals which remain active in the region throughout the year. Or it may consist in the shedding of the sensitive leaves of deciduous trees, the production of seeds and dying down of annual plants, the going into hibernation of mammals and cold-blooded animals, or the migrating of birds. Species vary in their responses and resistances. Those that can not make the necessary adjustments can not exist, and so are not found in the regions where unfavorable conditions occur at some time during the year. Temperature must certainly be considered as effective at any time of the year, not just during the reproductive period. A temperature law that does not take this into consideration obviously can not be a complete nor even a true statement of the controlling role of temperature in distribution.

Significance of Isotherms. Merriam found a rather close agreement between the isotherms of accumulated daily temperatures with the northern boundaries of his life zones. This, he maintained, was a proof that they were the effective temperatures involved in limiting northward distribution. That this is not necessarily so is shown by the work of others.

Livingston and Shreve (1921), also using the cartographic method in much the same way that Merriam did, attempted to analyze the temperature factor in all its phases as it affects the distribution of plants. They considered Merriam's temperature laws and life zones in detail. The aspects of the temperature factor which they considered were: duration of average frostless season; duration of average frost season; length of period of high daily mean temperatures; length of period of low daily mean temperatures; summation of daily mean temperatures above 0° F., 32° F., 39° F., and 50°F.; summation of exponential indices of temperature efficiency; summation of physiological indices of temperature efficiency; absolute temperature maxima; absolute temperature minima; average daily temperature during fourteen coldest days of year; Merriam's average temperature during hottest six weeks of year; and mean annual temperature. With all of these different aspects of the temperature factor, they found an east and west zonation of temperature across the continent. By selecting the proper isotherms, agreement in nearly all instances with the boundaries of the life zones can be had in a rough way. The selection of any one of these phases of the temperature factor, to the exclusion of the rest, as the effective one in controlling distribution, is not warranted without a basis in the physiological and behavior responses of the organisms concerned. This is the next point that needs to be considered here.

Summing Temperatures. Probably Merriam was right in assuming that the completion of any growth stage or mature organism requires a certain more or less definite amount of energy transformation. Krogh (1914) found this to be true for the pupal development of a beetle, *Tenebrio*, as measured by the total carbon dioxide output, and this output is not directly proportional to the temperature. In regions where the season is too short to allow the accumulation of the necessary amount of energy for the development of an organism, that organism could not, of course, be a regular member of the biota there. One may easily imagine that this may be one out of several factors effective in limiting the distribution of cold-blooded (poikilothermic) organisms (but not warm-blooded or homoiothermic ones as will be shown later). The difficulty comes in developing methods for computing this energy.

Merriam attempted to compute this energy requirement by the direct summing of daily mean temperatures above a certain threshold. Merriam quotes DeCandolle's work in 1835 as showing that wheat does not germinate at temperatures below 43° F. (6° C.), and so this temperature is the threshold for development in this species. Assuming that this temperature threshold is the same for all plants and animals and in all localities, Merriam's idea was to substract 43° F.

(6° C.) from the mean temperature for each day during the entire reproductive season. These temperature remainders would all be added together, and the resultant figure was to represent the total heat (in degree-days) available for development. By summing the effective temperatures in this way at a large number of stations he could arrive at totals characteristic of each life zone. Since different species of plants and animals apparently require different amounts of heat (energy) for their development, those that require the most would, he argued, be confined to the more southern life zones, while those that could get along with less would flourish in the more northern life zones. This is the physiological assumption for his first temperature law, the errors in which are pointed out in detail by Shelford in the succeeding paper.

However, there are criticisms that may be brought against this method of computing the total heat or total energy required for development in addition to those discussed by Shelford. The first of these is in regard to the selection of 43° F. (6° C.) as a threshold for development. The temperature threshold of development and activity is not the same for all organisms. Sanderson and Peairs (1913) estimated that the threshold value for the development of insect eggs and pupae varied from 37° F. to 52° F. in the case of different species. DeCandolle, himself, is quoted to have found seeds of some plants germinating at 32° F. while others, as corn, did not do so below 48° F. In the case of the development of eggs of the domestic fowl, the threshold temperature is 68° F. (Edwards, 1902). Likewise the initiation and termination of dormancy (hibernation and aestivation) in mammals has been found to occur at different temperatures and under different conditions (Johnson, 1931).

The temperature threshold may not be a constant value even within the same species. Shelford (1927) found that in the development of the codling moth the true temperature threshold is not a fixed point but varies, within certain limits, with the humidity and other weather factors, and also with the generation and the individual. For the larva, it was found to vary from 43° to 48° F.; for the pupa and egg, from 44° to 49° F.; and for the hibernated larva, from 43° to 50° F. We have reason to believe, also, that the temperature threshold is lower for plants and animals at high latitudes and altitudes than it is for those living in warmer regions. The error of selecting at random the threshold value for one species to hold for all forms in all localities is therefore manifest.

The table of summed daily temperatures (discussed above) which Merriam presents in his paper and which was used as the basis for drawing his isotherms is incorrect. This was due to a misunderstanding with the U. S. Weather Bureau, which computed the temperatures. The error in these computations was not discovered until later (Merriam, 1899), and no corrected table has since been published. The temperatures were summed above a threshold of 32° F. (0° C.) instead of 43° F. (6° C.), although only for days when the mean temperature arose above 43° F. (6° C.). Consequently the table of summed temperatures which Merriam gives is much too high, as Shelford points out graphically in the succeeding report. The agreement between Merriam's isotherms and the boundaries of the life zones is not a proof, therefore, of the correctness of his arguments—rather the contrary.

Various methods have been devised for summing temperatures above a definite threshold. The earliest method, and that which Merriam used, was formulated by Reaumur (1735) who summed temperatures above freezing for the years 1734 and 1735 and correlated these temperatures with the difference in the time of appearance of plants and animals during these two years.

From the practical standpoint, this method is criticized because the sums which it yields are too variable. Seeley (1917) summed temperatures above 43° F. from January 1 to the date of ripening of the Crawford peach at Wauseon, Ohio, for the years 1883 to 1912. He obtained sums during certain years as widely different as 3030° and 4347° F. He therefore declares that this method has no great value. He further emphasizes the importance of considering the temperature of the plant itself rather than of the air when studying the influence of temperature on growth. Likewise, Hunter and Hooker (1907) determined the total "effective temperatures" for the hatching of eggs of the cattle tick, by direct summing of temperatures above 43° F., and found that eggs laid from September 15 to October 15 require a total of 837.6° to 1510.8° F. to hatch, while those laid in April and May require 981.6° to 1139.1° F.

Livingston and Shreve (1921) and Shelford (1927, 1929) have severely criticized from the physiological viewpoint the method of direct summing of air temperatures for ascertaining the accumulation of energy for development. This is based on the fact that the rate of development varies widely at different temperatures. The inaccuracy of the method of direct temperature summation is fully dealt with in the following paper and so will not be discussed further here. The

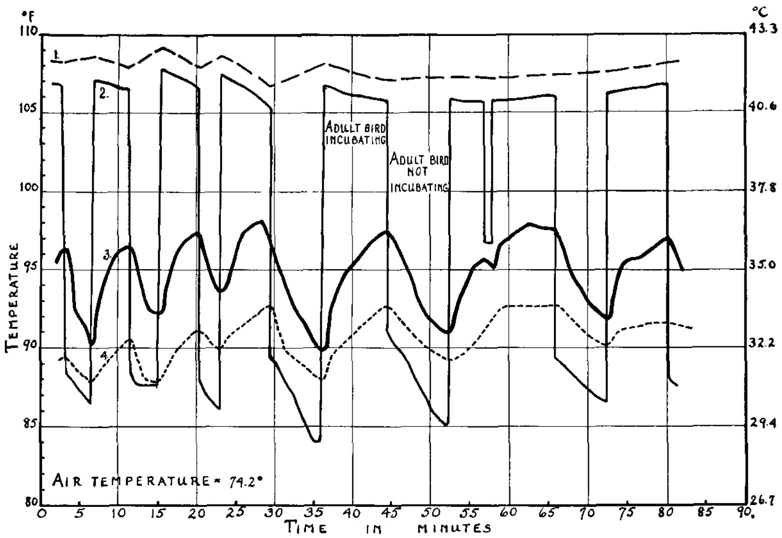

FIG. 27. Natural fluctuations in temperature of a House Wren egg under normal conditions in the nest. Curve 1 represents the body temperature of the adult bird; curve 2 is the temperature in the nest above the eggs, both when the bird is incubating and when she is away; curve 3 shows the temperature of the egg; and curve 4 shows the temperature in the nest beneath the eggs.

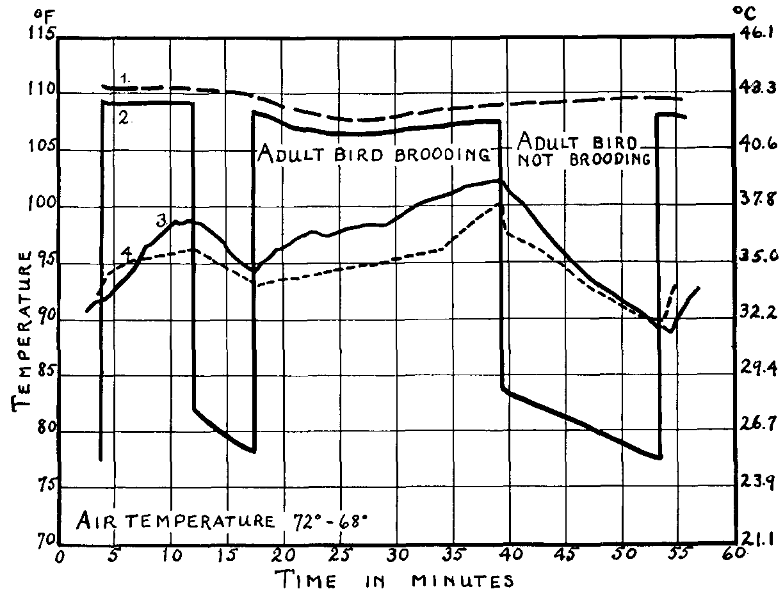

FIG. 28. Natural fluctuations in temperature of a House Wren nestling under normal conditions in the nest. Curve 1 shows the body temperature of the adult bird; curve 2 shows the temperature in the nest above the nestling, both when the adult bird is brooding and when she is away; curve 3 shows the temperature of the nestling; and curve 4 is the temperature of the nest beneath the nestling.

complexity of the problem is evident, and much more work needs to be done before the actual limiting effect of "total heat" during the season of reproduction may be adequately conceived.

Temperature Tolerance by Birds. A certain rather definite total of energy is probably as necessary for complete embryonic development of birds as it appears to be for the development of other animals (Krogh, 1914; Shelford, 1927). Bohr and Hasselbalch (1900) measured the rate of carbon dioxide output at all stages of the development of the domestic fowl, and similar studies have been performed by others (see Needham, 1931). The subject is capable, therefore, of experimental proof and measurement. Bird's eggs develop to hatching within a narrow temperature range. They are dependent, therefore, upon suitable conditions for maintaining them within this range.

Merriam's temperature law assumes that a sum of environmental temperatures is required before this total energy required by the bird's egg for development can be obtained. Actually, however, the temperature of the bird's egg in the nest is maintained several degrees above that of the air and is relatively unaffected by outside environmental temperatures. This is well shown in figure 27, which is taken from a forthcoming paper (Baldwin and Kendeigh, 1932) where the subject is discussed in detail. Likewise, the temperature of nestling birds is not directly dependent upon that of the outside environment (Fig. 28). The reason for this is that the adult birds have evolved a complicated nest and reproductive behavior that keeps nest conditions, particularly those involving temperature, at what is probably the optimum for the species. As long as the adult birds are able to survive and carry on normal activities in a region, they can maintain the requisite conditions required for the proper development of the young regardless of any accumulation of environmental temperatures without. This constitutes one important difference in the developmental history of warm-blooded and cold-blooded organisms, since the latter alone are directly dependent upon environmental temperatures for furnishing the energy needed in development. Thus summed environmental temperatures, even if such summed temperatures could be correctly determined in a significant manner, cannot possibly limit the distribution of birds through affecting development. Temperature appears to limit the northern distribution only when it affects the adult, and here other aspects of temperature are more important.

Some ornithologists have interpreted Merriam's laws as meaning that a certain sum of environmental temperatures during the season is required before the adult bird is able to complete its entire nesting cycle. This idea is without adequate physiological basis for warm-blooded animals. As long as temperatures are above the limit of tolerance for the existence and carrying on of normal activities by the adult birds, the exact degree of heat, while it has some importance, is not of primary significance. Birds have been found in our studies of body temperature regulation to have efficient physiological mechanisms that compensate for variations in environmental temperatures and maintain constant body temperatures (Baldwin and Kendeigh, 1932).

The length of the season when temperatures are above the threshold for development and activity of cold-blooded animals and of plants or above the limit of tolerance for adult birds and mammals is quite a different matter from the summation of daily temperatures during this period. The season may be too short for allowing the completion of the entire reproductive cycle of activities. This may conceivably determine whether the bird will raise each season two broods, one brood, or none at all. It is only when the temperatures go beyond the limits of tolerance that birds are incapable of reproducing or of existing in the region and are limited in their distribution.

Birds possess a limit of tolerance to low air temperature when this factor acts in conjunction with long periods of time during which the obtaining of food is difficult. We have made an intensive study of temperature resistance of birds (Kendeigh, Ms.). These studies indicate that the average night temperature combined with the number of hours of darkness, when the procuring of food is impossible for most birds, are crucial and critical factors involved in controlling the northward distribution, the migration, and the abundance of birds. This is particularly true of the smaller passeriform species. Larger and heavier birds may have a greater resistance to low temperature than do the smaller birds, and this can be measured. Some factors other than temperature are correspondingly more important with the larger birds than the smaller ones, although other factors must be considered also in the case of all species.

Other Factors. Other factors aside from temperature may be of more or less critical importance in limiting the distribution of plants and animals. Undoubtedly, different factors have diverse degrees of importance with different species. It is advisable to study each of these other factors separately for each species of birds before broad generalizations be made concerning whole faunas. Our own experiments with birds emphasize the importance of such other factors as relative length of day and night, intensity of solar radiation, vegetation, food, and biotic competition (Kendeigh, Ms.). Livingston and Shreve (1921) have discussed the importance of many different factors in relation to the distribution of plants; Grinnell (1914, 1917, 1928) and Howell (1922, 1924) have done the same for mammals and also birds.

Summary. The criticisms against Merriam's first temperature law as it applies to both animals and plants may be summarized as follows:

(1) Temperatures at other times of the year than the season of growth and reproduction may be effective in limiting the northward distribution of organisms.

(2) The mere cartographic agreement between particular lines of equal temperature (isotherms) and boundaries of life zones or other biotic areas does not in itself without adequate physiological basis constitute proof that such particular factors are the critical ones limiting distribution.

(3) The physiological basis of summing temperatures, which Merriam used, is without significance because (a) the temperature threshold of development varies widely in different species, and so, no one value which is not an average for each locality can be used; (b) temperatures, as they affect in a significant manner the development of plants and animals, cannot be summed directly because of marked differences in the rate of development at different temperatures; and (c) no distinction between cold-blooded and warm-blooded organisms is made in the possible effect of environmental temperatures upon development.

(4) The actual statistical climatic data used by Merriam to support his arguments and to prove the relation between temperature and the distributional boundaries of the life zones were incorrectly determined.

(5) Other phases of the temperature factor or other factors aside from temperature are of importance in limiting the northward distribution of animals and plants.

The Second Temperature Law

The arguments concerning Merriam's second temperature law will be only briefly summarized here. This law states that the southward distribution of plants and animals are limited by the mean temperature during the hottest part of the summer.

Isotherms. The same criticism which holds against the method of Merriam in demonstrating the first temperature law applies also in the case of the second temperature law. The mere agreement between particular isotherms and limits of distribution does not, without adequate experimental and physiological basis, constitute proof that such factors are the most critical or controlling ones.

Maximum Temperatures. In our study of the physiology of bird temperatures (Baldwin and Kendeigh, 1932), we found that variations in the mean temperature of the air from day to day have very little effect upon body temperatures of birds, even during the hottest period of the summer. However, during periods lasting from one to a few hours, the temperature of the bird may rise and normal nesting behavior be greatly disturbed due to exposure to the sun or to maximum daily air temperatures. Experiments performed with English Sparrows (*Passer domesticus domesticus*) and Eastern House Wrens (*Troglodytes aedon aedon*) indicate that high air temperatures become significant only when they get as high as 93° F. (Kendeigh, Ms.). At air temperatures above this degree the resistance time of birds decreases, body temperature may rise, the general metabolism is abnormally disturbed, and normal reproductive behavior interferred with. These two species of birds frequently survive air temperatures above 93° F., but only when these temperatures are maintained for relatively short periods each day and only by modifying their normal behavior. Birds have, therefore, upper limits of temperature tolerance as well as lower limits, and these are effective in controlling distribution (Kendeigh, Ms.).

However, these high air temperatures usually do not persist for more than a few hours each day. They are the maximum daily temperatures. The mean daily temperature, even during the hottest part of the summer, is considerably lower, because the nights are cooler. On the basis of these experimental results and careful analysis of the temperature factor in the field, the conclusion appears warranted that the maximum daily temperatures, rather than the mean, are more important in controlling the southward distribution of birds. We may suppose that the same is true with other kinds of organisms.

Other Seasons. Merriam limited the influence of high temperature to the hottest part of the year (six weeks). While high temperature is undoubtedly of considerable significance at this time, especially in the control of the breeding range, its possible effect at other seasons must not be excluded. High temperatures may have an influence in determining the southward distribution of northern birds in the winter, although there is little conclusive evidence on this point. Likewise, during both the spring and fall migrations, the distribution of a species at any one time may be influenced by high temperatures.

Other Factors. Mention needs to be made again that other factors aside from temperature (such as those enumerated above) may often exert an important role in controlling the distribution of birds and other organisms, even in a southerly direction (Grinnell, 1914, 1917, 1928; Howell, 1922, 1924; Kendeigh, Ms.; Livingston and Shreve, 1921).

Summary. The arguments against Merriam's second temperature law maintain that:

(1) The mere agreement between isotherms and the distributional boundaries of life zones is not proof without adequate physiological basis that such factors are the controlling ones in distribution.

(2) Daily maximum temperatures are more important than daily mean temperatures in controlling the southerly distribution of birds and probably other organisms.

(3) High temperature may influence the distribution of organisms at other seasons of the year than just the six hottest weeks during the summer.

(4) Factors other than temperature are also important.

Temperature Laws and Life Zones

If Merriam's temperature laws can not be accepted and used, the question may be raised as to what effect this will have upon the reliability of the "life-zone" concept and the maps of life zones that have been made by ornithologists and mammalogists.

It is difficult to estimate to what extent these temperature laws have influenced the mapping of life zones. It is certainly true that Merriam published two life zone maps of North America (Merriam, 1890, 1892) before he definitely published the temperature laws in 1894. The earlier maps seem to have been based largely upon the known distribution at that time of genera of plants and animals, although the importance of temperature was even then appreciated. Certain modifications in the maps published in 1894 and later years suggest that after the isotherm map was made, secondary changes in the boundaries of the life zones may have been thought advisable. Only in so far as the life zones are based upon these temperature formulae of Merriam, is their inadequacy questioned at this time. If the life zone concept is to continue to exist, it must be entirely upon the basis of the actual distribution of animals and plants. Recent maps of life zones appear, as far as we can judge, to be based largely upon actual distribution of organisms, although the organisms selected to characterize the different life zones are frequently of such minor importance and abundance as to be without significance for correlations with climatic conditions.

Conclusions

1. Merriam's two laws of temperature control for the northward and southward distribution of animals and plants cannot be accepted.

2. The life zone concept, in order to survive, must be based upon the actual distribution of important and significant animals and plants in nature and not upon climatic factors of uncertain preconceived importance.

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