THE RELATION OF TEMPERATURE TO THE HIBERNATION OF INSECTS

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Three years ago at the Philadelphia meeting of this association the writer advanced a hypothesis for determining the time of maximum emergence of the Mexican cotton boll weevil. Subsequent observations by others have tended to discredit the correctness of the method then advanced, but it served to call attention to the fact that "the time of emergence of insects from hibernation and the date upon which they begin oviposition or normal activity is dependent upon well-defined physical laws" which should be determined, and the writer is of the opinion that careful study of the large amount of data now accumulating concerning the time of emergence of the boll weevil will reveal the laws governing the time of its appearance.

Since then, with the aid of assistants and students, I have made a number of experiments principally with the tent caterpillar (*Malacosoma americana*), the brown-tail moth (*Euproctis chrysorrhoea*), and the codling moth (*Carpocapsa pomonella*), in an endeavor to determine the relation of temperature to the hibernation of insects. Only a beginning has been made and as we get deeper into the subject we find that it is an exceedingly complex one and is closely bound up with fundamental problems of physiology and heredity. There are a few points, however, which may well be brought to your attention at this time.

It has been customary in the study of meteorological and biological data concerning temperature to use the mean daily temperature in accumulating the amount of temperature involved in any phenomena. But it is evident that if the day be cloudy and the sun shine for a short time at noon that the mean for that day will be much higher than the actual mean temperature which occurred during that day. We have therefore resorted to the use of recording thermographs of the Reichard or Short and Mason type, such as are in use by the U. S. Weather Bureau, which, with frequent standardization, show the actual temperature for the whole day. The polygon covering the temperature for the day is then measured with a polar planimeter and the actual mean temperature for the day is thus secured. It is found that frequently a difference of ten degrees occurs in greenhouses between the mean secured from the maximum and minimum and the true mean thus secured with a thermograph. Such records are especially important where a glass house is being used for experiments, and it would seem that this is the only accurate method of recording temperature where an exact study of temperature is desired for bio-

logical work, if not indeed for meteorological studies. The weekly sheets are readily filed and the temperature which occurred at any time during breeding experiments can thus be readily referred to or computed in the future.

We have been endeavoring to determine whether there be a "thermal constant" which governs the emergence of insects from hibernation. The "thermal constant" for insects may be defined as *that accumulation of mean daily temperature above the "critical point" of the species, which will cause it to emerge from hibernation or to transform from any given stage.* The "critical point" above which the temperature is accumulated is a matter of vital importance and seems to have been largely neglected in entomological work. European botanists have established the critical points of a long list of plants and shown that a large variation exists between species.^a The "critical point" may be defined as that point of temperature above which active metabolism occurs and above which the accumulation of temperature affects the time of definite transformations in the organism, such as the leafing and flowering of plants, and the emergence from hibernation, hatching and transformations of insects. In recent studies of the relation of temperature to insect life it has been assumed that all temperatures over 43° F. are "effective temperatures," or that 43° F. is the critical point. But the records based upon this assumption go to prove that the critical point varies and that it must be determined for each species before accurate conclusions concerning the relation of temperature to that species can be secured. Thus, as was pointed out by Simpson in his excellent studies of the Codling Moth, it was impossible for him to draw definite conclusions from a considerable mass of data published by him concerning the influence of temperature upon the duration of its various stages.^b The same fact has been brought out by Hunter and Hooker in their recent paper on the North American Fever Tick in their study of the relation of temperature to the period of incubation.^c In the case of the brown-tail moth, our present observations go to show that 34° F. is the critical point above which the temperature accumulates in determining the time of emergence in the spring. The critical point is doubtless much lower for northern species and much higher for southern species, and it seems quite probable that it may vary for the same species which has become acclimated to diverse climatic conditions. Thus the

^aSee Cleveland Abbe, First Report on the Relations Between Climates and Crops, Bulletin 36, U. S. Weather Bureau, 1905.

^bSee Simpson, Bulletin 41, Division of Entomology, Tables IV and V, pages 37-39.

^cHunter and Hooker, Bulletin 72, Bureau of Entomology, page 20.

tent caterpillar has but one generation both in the North and South, hibernating over winter in the egg, in which the larva is completely formed. The critical point must be much higher in the South, for the low temperatures which are effective in the North are rarely reached in the South.

The time at which insects enter hibernation in the fall is undoubtedly largely influenced by temperature, and in many species it may be the controlling factor, but there are many cases where hibernation commences before there is a material drop in temperature, and that the lowering temperature is the controlling factor is disproved by the fact that insects subjected to high temperatures before the normal time for hibernation persist in hibernating or else remain slightly active, but rest and do not feed or reproduce for a considerable length of time. This has been shown by Tower in his remarkable experiments upon the Potato Beetle and in our own experiments. This paper of Dr. Tower^d will ever remain an entomological classic and should receive the study of everyone interested in economic entomology. Tower has shown that all of the beetles of this genus have two generations and no more, and that after the second generation there must be a time of rest before reproduction continues. In some cases this is hibernation and in others aestivation, which Tower maintains are practically the same as regards the life history of the insect. In both cases the insect prepares for the resting stage by losing about 30% of its gross weight through the loss of water, which enables it to withstand a lower freezing point and higher temperatures than if the protoplasm were not thus condensed.

In endeavoring to determine the thermal constant for emergence we have placed the hibernating stage in greenhouses heated at different temperatures and compared the amount of temperature accumulated in each up to emergence with that accumulating in nature. The first year the insects were not placed in the greenhouse until in January, after they had been subjected to considerable cold weather. They emerged in due time in a fairly normal manner. In 1906 the insects were brought into the greenhouse earlier in the season before they had been subjected to much cold out of doors. As a result it required much more heat over a longer period to force their emergence and they emerged irregularly for several weeks. Lots brought in later in the winter emerged much more normally. We were therefore led to suspect that the cold of winter had a positive influence in determining the length of the hibernation of these insects, which subse-

^dW. L. Tower, Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*. Carnegie Institution, No. 48. 1906.

quent experiments have proven to be true. This fall we placed several lots in an icehouse and in cold storage for various lengths of time during August and September, at the same time placing other lots in glasshouses, where they never were subject to low temperatures. Those which were placed in cold storage have hatched, in the case of the tent caterpillar eggs in about two weeks, while those which have not been subjected to cold have not hatched yet. Several lots placed in storage and taken out at different times have proven this, and our experiments are arranged to show how long they must be subjected to low temperature and whether extreme low temperatures have any more effect or will reduce the time of hibernation more than those merely below the critical point. This fact had been previously shown by Weismann in his paper, "On the Seasonal Dimorphism of Butterflies" nearly thirty years ago,^e when he described experiments in which by subjecting pupæ of the summer form of *Pieris napi* to refrigeration for three months and then bringing them into a hothouse he was able to secure the winter form by about October first, but in which he was unable to secure the immediate transformation of pupæ of the fourth brood of *Araschnia levana* (*prorsa*) by placing them in a hothouse as soon as the pupæ formed, for invariably nearly all hibernated over winter, even in the warm hothouse, and emerged in the spring as the winter form. It is evident that subjecting these hibernating forms to low temperatures has the effect of producing a more complete rest than when hibernation goes on at higher temperatures, and the time of hibernation may therefore be shortened in many instances by subjecting to cold before heat. It is interesting to note in this connection that the same effect as that normally sustained by freezing has recently been secured with rhubarb, various bulbs, lilac and other flowering plants, by anesthetizing them with ether. The exact effect of the ether has not been definitely determined, as far as I can ascertain from a cursory examination of the literature, but Dr. Loeb^f has suggested that the effect is possibly related to the effect of cold upon chrysalids as mentioned above. If the effect of the ether is a drying process, as some claim, this seems possible.

In the light of these facts, may it not be possible to account for the fact that some insects have but a single generation in the South, while others have several generations? Thus the tent caterpillar, peach borer, plum curculio, canker worms, gypsy and brown-tail moths, and others, mostly insects affecting native fruits and seemingly indigenous

^eAugust Weismann, *Studies in the Theory of Descent*, translated by Meldola. Eng. Ed. London, 1882.

^fLoeb—*The Dynamics of Living Matter*. 1906, page 112.

FIGURE 1. Caption on opposite page.

to north temperate climates, have but one generation in the South, while southern species have many generations in the South, but the number decreases as they spread northward. Why should not all have several generations in the South? I have been unable to find any investigations of this problem whatever and would be indebted for any data which will throw any light upon it.

In some cases, however, the time of emergence from hibernation is controlled by moisture conditions as well as temperature, or independent of temperature. Thus Tower kept the potato beetle in hibernation for 18 months at a high temperature but with a dry atmosphere, and they emerged as soon as normal moisture conditions were produced. Webster and Hopkins have shown a similar effect of lack of rainfall on the emergence of the Hessian Fly in the fall. In relation to hibernation in humid climates the matter of moisture is probably not a controlling factor, but undoubtedly has the most important influence upon the time of emergence of forms in æstivation during the summer or in arid regions.

A principle which should be considered in any attempt to fix a thermal constant is the law of the velocity of chemical reactions. In general, it may be stated that the velocity of chemical reactions doubles or triples with every increase of 10° C., or in other words, a reaction will take but one half or one third as much time with an increase of 10° C. The application of this law to the velocity of various phases of the physiology of animal and plant life is receiving considerable attention by physiologists at the present time and some of the observations made are shown graphically in figure 2. But all of the observations made go to show that this so-called law is only an approximation of the facts between certain degrees of temperature ranging within 15° or 20° C. of the optimum temperature of the form under study. At low temperatures the velocity rises very rapidly as temperature increases, and above the optimum the velocity decreases. The difference between the observed change in coefficient of increase of velocity as temperature rises, as shown by these curves, and the theoretical application of this law if the velocity doubled or tripled with every increase of 10° C. is shown by the difference be-

FIGURE 1. Curves showing the relation of increase of temperature to the time required for stages of growth of animals, more particularly as affecting the emergence from hibernation and transformations of insects. *Hypothetical Curve*, indicating the empirical nature of the curve of effect of temperature of individual species; *V 2 and V 3 Curves* based on uniform coefficient of increase of velocity of reaction of 2 and 3; *Thermal Constant Curve*, based on thermal constant of 300° C. Numbers on curves are the thermal constants in degrees Centigrade at points marked. Optimum of 35° C. is empirical and varies for each species.

FIGURE 2. Caption on opposite page.

tween these curves and a horizontal line at 2 or 3, which would represent the plotting of the increase of velocity, were it uniform between the critical point and maximum.

If there be a thermal constant for all temperatures between the critical point and maximum, it would be represented by a curve like "T. C. C." in figure 1. But there is evidence to show that the thermal constant is lower at the optimum than at temperatures approaching the critical point. And if the velocity be plotted from the curve "T. C. C." of figure 1, the same curve in figure 2 shows that the coefficient of increase of velocity with a uniform thermal constant is much less than that observed, being only 1.5 at 25° C. On the other hand, if we plot a curve based on a uniform increase of velocity of a coefficient of 2 or 3 we secure curves V2.C. and V3.C. of figure 1, respectively, and by computing the thermal constant for various temperatures on these curves, it is found that the thermal constant increases below the optimum to a certain point and then decreases. Thus on V2.C. the thermal constant at 35° is 300, at 25° is 400, at 20° is 450, and then decreases to 400 again at 15°, to 300 at 10°, and at the critical point we secure the anomaly of a thermal constant of 80°, which is clearly impossible, as no reaction will take place unless above the critical point. The same would hold true of curve V3., or any other curve based upon a uniform coefficient of increase of velocity.

From a study of these considerations it seems probable that the effect of temperature upon various forms of animal life will be represented by a curve characteristic for each species or group for the various phenomena of growth considered, and that such a curve will be between the curve shown in figure 1 for the uniform thermal constant, T. C. C., and that for a uniform rate of increasing velocity, V2.C. Such a curve may be secured by a uniform coefficient of increase for the thermal constant as the temperature decreases from the optimum as shown in curve H. C.—hypothetical curve—figure 1.

FIGURE 2. Curves showing variation of coefficient of velocity of certain biological phenomena. *Hypothetical Curve*, based on same in figure 1; *Terrapin Heart Curve*, based on rate of heart beat of Pacific terrapin, from data by Snyder^a; *Thermal Constant Curve*, based on same in figure 1; *Toad and Frog Tadpole Curves*, based on rate of growth of toad and frog tadpoles from data of Lillie and Knowlton^b; *Frog Muscle Curve*, based on rate of contraction of gastrocnemius muscle of frog from data of Burnett^c; *Cat Heart Curve*, based on rate of beat of isolated cat hearts from data of Langendorff^d.

^a Snyder, Univ. Calif. Publications, Physiology, 2, pp 125. 1905, quoted by Arrhenius, *Immunochemistry*, pp 139.

^b Quoted by Morgan, *Experimental Zoology*, pp 260.

^c Burnett, *Jour. Biological Chemistry*, 2, pp 200-1906.

^d From Snyder, *Amer. Journal Physiology*, 17, pp 356-1906.

In this curve the thermal constant has been increased 25% for every decrease of 10° from the optimum or with a uniform coefficient of 1.25. Upon plotting this curve it is found that the thermal constant increases uniformly toward the critical point, but that it would approach the critical point to infinity. Upon plotting the curve of the coefficients of increase of velocity of such a curve, the curve H. C. of figure 2 is secured, which corresponds very closely with those secured from actual observations.

But if there be such an empirical temperature curve for each species or phenomenon, it is evident that there can be no thermal constant which will be constant at all temperatures, for it increases in a uniform ratio below the optimum. A constant may however be secured by reducing the increments of temperature for each unit of time to terms of the thermal constant at the optimum, which is therefore 1. Thus the values of one unit of time on the hypothetical curve, H. C., figure 1, would be 0.1 at 35° , the optimum, 0.056 at 25° , and 0.021 at 15° , etc. When by adding these values sufficient are secured to make 1, the thermal constant has been reached, equivalent to the thermal constant at the optimum temperature. To secure such values it would be necessary to secure the thermal constant at the optimum and at two or three constant temperatures below, upon which the curve of the species or phenomenon might be plotted and the values for each degree of temperature for one unit of time calculated.

At present this is, of course, largely a hypothesis, but it accords with all the facts which have come under our observation, and seems worthy of attention by those who are engaged in study of the relation of temperature to insect life; for without hypotheses what could we accomplish in such work? During the coming year we hope to definitely determine this matter by rearing large numbers of two or three common household pests in specially constructed apparatus which will maintain constant temperatures, and thus enable us to secure the thermal constants for various temperatures, which may then be compared with the amount of temperature accumulated with varying temperatures.

It may seem to some that such studies are of rather remote importance to practical economic entomology, but as such work accumulates it becomes more and more evident that a positive knowledge of these fundamental factors governing the life of insects may have great practical value, and that entomology, as well as all biological science, must consider its relations to the more exact and fundamental sciences of physics and chemistry, if we are to have exact knowledge of the life with which we are dealing. Hunter and Hooker have recently suggested the practical application of such work in their study

of the relation of temperature to the incubation of eggs of the cattle tick and it seems probable that a similar application might be made in determining the time of treatment of the codling moth, though it is hardly probable that it will be necessary in the latter case.

But it is upon a positive and not merely hypothetical knowledge of such controlling forces as temperature that our science must rest and no one can foresee what entirely practical application may be made of it in the future study of new pests as they present themselves for study under new conditions.

The remainder of the proceedings of the 20th meeting of the Association of Economic Entomologists will be given in the next number of the Journal. It has been deemed advisable, in view of its close relation to two papers in this number, to publish at the same time Mr. Hooker's summarized account of our knowledge of the role of ticks in the transmission of disease. The paper was prepared originally for presentation at the meeting and as a part of the symposium on ticks, consequently it is very fitting that it should appear at this time.

A REVIEW OF THE PRESENT KNOWLEDGE OF THE ROLE OF TICKS IN THE TRANSMISSION OF DISEASE*

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Not until within the last decade has the importance of insects and related animals as agents in the transmission of disease been fully appreciated. Within this period, however, the progress of our learning has advanced at an astounding rate. It was but fifteen years ago that Smith and Kilborne first demonstrated the role that the cattle tick, *Margaropus* (= *Boophilus*) *annulatus*, plays in the transmission of Splenic or Texas Fever of Cattle, and only ten years ago that Ross first employed *Anopheles* in his mosquito-malaria experiments. To-day we all know of the mechanical and biological agency of the flies and mosquitoes in the transmission of typhoid fever, cholera, anthrax or charbon, nagana or tsetse-fly disease, surra, malaria, yellow fever, filariasis and dengue, and of fleas in the transmission of bubonic plague. Together and with the investigation of the Bacteriologist and Protozoölogist has come that of the Entomologist in the study of the life history and habits of the disease-carrying insects. We are all acquainted with the investigations in this country of Dr. L. O. Howard,

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