Summary

1. The following free sugars were identified in alcohol extracts of Connecticut lake muds: sucrose, glucose, galactose, fructose, arabinose, xylose and ribose. Glucose was the most abundant free sugar. It occurred in concentrations of 13-191 mg per kg dry weight of ethanol-insoluble sediment.

2. A direct linear relation was found to exist between free sedimentary hexoses and summer seston chlorophyll in the surface muds of four Connecticut lakes.

3. A principle of diagenesis was developed and applied to data for sedimentary free sugars and sedimentary chlorophyll in a profile from Bethany Bog, Connecticut. It is concluded that free sugar is destroyed at a faster rate in lake muds than sedimentary chlorophyll.

4. The free sugars of sediments do not all directly arise from the free sugars of plants, but rather appear to be at least partly breakdown products of polysaccharides.

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DEVELOPMENT OF AEDES (DIPTERA: CULICIDAE) AT FORT CHURCHILL, MANITOBA, AND PREDICTION OF DATES OF EMERGENCE[1]

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Introduction

A program of biological and control studies on biting flies has been conducted since 1947 at Fort Churchill, Manitoba (Hocking *et al.* 1950; Twinn *et al.* 1948; Twinn 1950; Twinn *et al.* 1950). The planning of biting-fly control programs for military areas in the Canadian north (Brown *et al.* 1951; Twinn *et al.* 1950) has indicated the need of more basic information on the ecology, development, and behavior of pest flies. The effectiveness of large-scale chemical control programs depends largely on the proper timing of applications of the insecticide. During the planning stage especially, information on population peaks and on seasonal variations in insect behavior related to the environment is important when control operations are limited to one or two applications. In the fly-infested areas of the north, where chemical control for the protection of small field parties is not practical, some interest has also been shown in the possibility of using periods of relative inactivity of certain pest flies for carrying out field operations.

Studies on the behavior of the immature stages of mosquitoes in subarctic environments have been described, Haufe, to be published, a). Coordinated studies during the same period (1949-52) were designed to ascertain the rate of development of mosquitoes in relation to subarctic environments. The possibility that there are two relations involving the environment of developing stages of mosquitoes is discussed in this paper on

[1] Contribution No. 3286, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada. The results herein reported were obtained by the Entomology Division in a program of studies on the biology and control of biting flies being carried out on behalf of the Defence Research Board, Canada Department of National Defence, and with the co-operation of that organization and other agencies.

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the basis of continuous seasonal observations on pools in a natural mosquito habitat. These relations may exist (i) between rate of development and thermal conditions of the environment and (ii) between thermal conditions of the environment and meteorological phenomena. Mathematical relations between development and environmental conditions have been suggested by Blunck (1923) and Bodenheimer (1927) for insects on the basis of environmental air temperatures. Apparently use of mathematical devices in estimation of development of mosquitoes has not been described previously.

Accurate prediction of adult insect emergence depends on the variation that may be expected (i) in assessment of effects of environmental factors on rate of development, and (ii) in measurement of meteorological and edaphic factors that are known to influence rate of development. The development of dry-land insects is usually subject to considerable, and frequently to extreme, degrees of variation; but organisms developing in water are less subject to extreme fluctuations in the environmental factors that may be difficult to measure. The object of the studies described in this paper was primarily to determine variabilities in those factors that may be important in estimating the periods of emergence of northern mosquitoes.

Mosquitoes found in the Fort Churchill area include the following species: *Aedes impiger* (Walk.) (= *A. nearcticus* Dyar; Vockeroth 1954), *A. nigripes* (Zett.), *A. punctor* (Kirby), *A. hexodontus* Dyar, *A. pionips* Dyar, *A. excrucians* (Walk.), *A. flavescens* (Müller), *A. campestris* D. & K., *A. cinereus* Mg., and *A. communis* (Deg.). All these species except possibly *A. communis* habitually bite man in this locality. Although not considered a pest in the area under observation, *A. communis* was selected for study for several reasons: (i) It was the only species to be found easily in pure or nearly pure colonies in the number of pools necessary for a comparative study on thermal environment. (ii) It was the most abundant species in the immature stages; studies in individual pools might be conducted with large samples of populations since the larvae often exceeded 25,000 in a single pool. (iii) The species tolerates large variations in several edaphic factors, a characteristic that enhances the value of observations on the development of a species in various types of environment (Haufe 1952). (iv) Studies on behavior of *A. communis* larvae indicated that patterns of behavior related to geophysical factors may influence the dependence of rate of development on certain thermal conditions of the environment (Haufe, to be published, a). (v) Comparative studies on the patterns of behavior of species listed as serious biters indicated that the 'blacklegged' species of *Aedes* (*A. impiger, A. nigripes, A. punctor, A. hexodontus, A. pionips,* and *A. communis*) were qualitatively the same in this respect; the only interspecific variation in pattern of behavior appeared to be in the degree of aggregation (Haufe, to be published, a). Aggregations were not observed for *A. excrucians, A. campestris, A. flavescens,* and *A. cinereus;* but the numbers of immature stages of these species in individual pools were possibly too small to exhibit noticeable aggregations. Some species such as *A. campestris* and *A. flavescens* selected shallow, muddy pools less than two inches deep. In this type of habitat the horizontal and vertical temperature gradients common to deeper pools (Haufe, to be published, a) may be insignificant or even non-existent.

Of the species mentioned above, the 'blacklegged' group of *Aedes* was of primary economic importance in the north where the protection of military camps was concerned. Our investigation of the possibility of early prediction of emergence of mosquitoes was chiefly directed toward these species. Although preliminary reports (Hocking *et al.* 1950; Twinn *et al.* 1948) have described the general life cycle of these mosquitoes, it should be emphasized that the 'blacklegged' group in the Subarctic is univoltine. Beckel (1953) found that eggs recovered from pools following the summer period of oviposition would not hatch before they were subjected to low temperatures. Eggs hatch very quickly and larval development is rapid however in the spring with the first exposure of eggs to open water at pool margins. These species therefore have a diapause in the egg stage that has the effect of telescoping the life cycle of post-hatching stages into short periods of mass-development. Consequently the emergence of each species is marked by sudden increases in the adult mosquito population and the species also emerge in close succession to cause the rapid build-up of hordes of mosquitoes over a period of usually not more than six weeks each summer. These characteristics of the mosquito life cycle are advantageous in the solution of problems of prediction on the basis of meteorological and environmental conditions.

Appreciation is expressed to W. N. A. McLean and J. A. Armstrong, Survey Assistants, Veterinary and Medical Entomology Unit, Ottawa, for assistance in the field work in 1951 and 1952, respectively, and to Lieut. K. R. Van Skike, Preventive Medicine Company, United States Army, for assistance in 1951; to G. F. Kennedy and other members of the Meteorological Division, Canada Department of Transport, Fort Churchill, Man., for co-operation in supplying special meteorological data and services; to Dr. C. R. Twinn, Head, Veterinary and Medical Entomology Unit, Ottawa, for valuable assistance; to Prof. F. P. Ide, University of Toronto, for advice in planning the work and reading the manuscript; and to Dr. F. J. O'Rourke and Dr. J. J. R. McLintock, Veterinary and Medical Entomology Unit, Ottawa, and others for reviewing the manuscript and making suggestions.

METHODS

Biological Method

The methods employed in the field studies had three objectives: (i) to investigate the effects of meteorological factors on the thermal conditions of a pool in so far as they influence the development of mosquito larvae, (ii) to describe mathematically the rate of development of a species of mosquito in relation to the thermal conditions of the environment, and (iii) to compare the rates of development of the pest species of mosquitoes in the area.

For (i) the studies were conducted in nine pools. These varied in size, shape, depth, and location, sinces it was important to measure the maximum variation in mosquito development that might be attributed to physical characteristics of the pool and to edaphic factors of surrounding terrain. The pools formed a series from the completely exposed type that is common on the tundra to the type partially sheltered by vegetation that is characteristic of the transition between tundra and Boreal forest. The sites used for these studies are described in detail in a previous paper (Haufe, to be published, a). The pools used for all phases of the study were typical of either tundra or forest-tundra transition in a permafrost area.

The meteorological conditions were recorded at the study site and supplemented when necessary by records from the weather station at Fort Churchill. Meteorological data included continuous records of air temperature, sunlight, humidity, wind chill, and wind speed. The thermal condition of the pool was recorded as the daily average temperature taken at a depth of one inch below the surface of the water in the deepest part of the pool. Experience indicated that for most temperature equipment accuracy of measurement was greater at one inch than at lesser depths. Continuous recordings of pool temperature were made in some of the pools by multiple-pen-type temperature recorders (Taylor, Series 75 J)[4] fitted with mercury-actuated bulbs and extensions; in other pools, maximum daily variations in temperature were recorded by maximum and minimum thermometers.

For (ii) the studies were restricted to seven pools, two in 1951 and five in 1952. In 1951 the investigation of the effects of thermal conditions of the environment on rate of development was combined with behavior studies of immature stages of *A. communis* (Haufe, to be published, a) in the same pools. Behavior patterns of mosquito larvae were related to their thermal environment; therefore the combined studies were arranged primarily to assess the accuracy with which mathematical "time x temperature" components[5] of development might be corrected for the effects of daily patterns of behavior. The behavior studies on the species had indicated (i) the temperature preferendum and (ii) an estimate of the amount by which pool temperatures in an insolated sector exceeded recorded one-inch temperatures.

Larvae and pupae were free in the pools during the major part of their development. When the pupae became more numerous than the larvae, a cage was erected near the middle of the pool in a position at which the water temperature equalled or nearly equalled the average one-inch temperature. Pupae that appeared to be ready to emerge were dipped into the cage daily; mature pupae of *A. communis* are easily distinguished by their flashing, white ventral parts. When the white scales are formed on the abdominal sterna of the nearly developed adult, the light is reflected from the white scales through the pupal skin. As the pupa works downward in the water in daylight a flash of white is discernible with each flexion of its abdomen. Usually pupae could be caged as little as a day before emergence of the adults by this method. The risk in this procedure is that density-dependent factors may influence the rate of development in a cage. We experienced high mortalities among larvae in overcrowded cages in previous surveys of northern mosquitoes. Gillies and Schute (1954) have also described some effects of overcrowding in laboratory cultures of mosquitoes. For this reason approximately 50 pupae only were added to the cage each day following the appearance of white ventral parts on the abdomen. We considered this procedure to be adequate since the form of distributions obtained for frequency of emergence in individual pools was nearly normal in all cases with consistent skewness to the right. Adults

[4] Taylor Instrument Companies, Rochester 1, New York, U.S.A.

[5] The "time x temperature" component of development is the theoretical product of time (in units) and temperature (in units) necessary for development to the adult after the thawing of the pool in spring.

were removed from the cages daily at the same hour. Males and females were segregated and frequency curves of emergence were drawn for each sex. The period of development was considered to be the time from the first appearance of open water in the pool to the peak of emergence for the adults trapped in the cage. This arbitrary delimitation was based on practical availability of meteorological data for widespread areas. Communication in arctic and subarctic areas in Canada is maintained primarily by light aircraft equipped with skis or pontoons. The break-up of ice along the shorelines of lakes and ponds is particularly important in the spring season in the briefing of pilots on military and civilian missions. The appearance of open water in pools and lakes is carefully documented geographically at aviation forecast offices for large areas from reports of pilots that arrive daily at both major and minor supply bases serving military and civilian outposts. The arbitrary selection of first appearance of open water to delimit the beginning of mosquito development is practical therefore from a meteorological point of view. Furthermore, the delimitation is biologically adequate since univoltine species of mosquitoes in the Subarctic hatch immediately with the thawing of pool borders (Haufe, to be published, a).

The development of *A. communis* was studied in 1952 by the same general procedure and with the same type of equipment. The selection of pools was modified, however, to get a series of developmental "time x temperature" components of various magnitudes. This was accomplished by selecting single pools at intervals of about a week, *i.e.*, the first pool was the one in which open water appeared earliest during the spring thaws, the second was one in which open surface water appeared approximately a week later, etc. The "time x temperature" components of pools selected in this manner were different on the basis of seasonal summations of meteorological conditions. The combined studies on the development of *A. communis* provided data for comparing rate of development with environmental temperatures under natural conditions.

For (iii) a study was carried out in 1952 by a procedure similar to that for (ii) except that the study was designed to compare rates of development of the species of mosquitoes common in the area. The development of each species was studied in at least three pools having different thermal characteristics, two to establish a relation between rate of development and environmental temperature and a third to provide a check on the reliability of the results. The data were treated in the same manner as for (ii).

Statistical Method

The interdependence of meteorolgical factors that contribute to the environment was recognized in all correlations. Conrad and Pollak (1950) recognized the need for this approach in solving climatological problems and reviewed methods and concepts that are useful primarily in representing climatological phenomena. They have pointed out the advantages and disadvantages of certain methods in relation to various geophysical problems. The environment of immature mosquitoes must be recognized as a complex of interdependent dynamic factors and this view plays an important part in the selection of a suitable statistical method. The coefficient of correlation (r) and its probable error (F) were used to evaluate the relation between meterological factors and the water in mosquito pools. Although the probable error does not meet with complete satisfaction as a test of significance under certain conditions, it has the advantage of accommodating the rare observations that may be termed *force majeure*. The probable error therefore is useful in testing correlations within extremely dynamic situations such as the natural environment of mosquitoes. The chief hazard in the analysis of relations between major factors in natural environments is the inevitable influence of unexpected inter-relationships that have to be considered as unavoidable accidents in the design of the investigation. Rare and unexpected events that cause discontinuities in the data from a field study affect the use of the probable error less than other tests of significance.

On the basis of confirmation by physical reasoning or other independent evidence "six times the probable error" has been accepted as the "rule of thumb" for avoiding false conclusions in correlations between natural elements. It is equivalent to odds of 10,000 to 1 as compared with 20 to 1 for "three times the probable error." "Three times the probable error' is accepted in the correlation of natural elements only when it is supported by other independent evidence. This criterion is not too severe when the purpose of the study is kept in mind. Individual geophysical factors may be expected to have little value in the practical prediction of mosquito development unless the correlation is very high.

Where X, T, Y, Z represent the variations in pool temperature (°F), air temperature (°F), daily sunshine (hours), and wind chill (kg-cal/metre^2/hr) respectively:

Coefficient (r) between pool temperature and air temperature is

$$r_{XT} = \frac{1}{n} \cdot \frac{\Sigma XT}{\sigma_X \cdot \sigma_T}$$

Probable error of the coefficient is

$$F = 0.6745 \times \frac{(1 - r^2_{XT})}{\sqrt{n}}$$

r is significant for rigorous purposes only if it is greater than 6 times the probable error.

Coefficient (r) between pool temperature variations (X) and air temperature variations (T) at constant daily periods of sunshine is

$$r_{XT.Y} = \frac{r_{XT} - r_{XY} \cdot r_{YT}}{\sqrt{(1 - r^2_{XY})\ (1 - r^2_{YT})}}$$

In Figures 1-3 inclusive the lines representing the *regression equations* are combined with the dot chart to provide visual indication of the degree of correlation. For example, in Figure 1 in which X and T represent pool temperature and average daily air temperature respectively, the deviations of X and T from the arithmetic mean are plotted in pairs on a cartesian coordinate system with origin (0, 0). The points (X, T) might be scattered in such a way that they cover the quadrants of the coordinates with greater uniformity as the number n of the pairs of deviations is increased. In this case no correlation exists between X and T. However in Figure 1, the dot diagram shows a crowding of the points into the first and third quadrants indicating a linear proportionality. This proportionality is represented by a straight line $T = bX$ that passes through the origin and is best fitted to the point cloud.

If T should be an analytic linear function of X, then $T - bX$ would be exactly zero. In this investigation this is not valid and the value of b must be determined so that the difference $T - bX$ becomes as small as possible. Since only the absolute magnitudes of the deviations, and not their signs, play any role in this problem, b should be chosen so that the sum of the squares of $T - bX$ is minimum. The condition is fulfilled if

$$\frac{d}{db}\Sigma(T - bX)^2 = 0,$$

and
$$b = \frac{\Sigma XT}{\Sigma X^2} = \frac{(1/n)\ \Sigma XT}{(1/n)\ \Sigma X^2}$$

The equation $T = bX$ contains the arbitrary assumption that X is the independent variable; but this assumption is not valid for this problem under the circumstances of the study. For instance, if X is the independent variable the air temperature (T) is considered to be influenced by the ground temperature and hence also by the pool temperature (X). In other words we know that radiation of heat takes place from the ground to the air during the night. But we also know that warm air masses moving over cold ground transfer heat to the ground and hence also to the pools. For the latter physical condition T must be considered the independent variable. Since there is a continuous alternation of these two physical conditions from day to day in the relationship between air temperature and ground surface temperature, two arbitrary assumptions must be included in the relation between the two variables, namely that either X or T may be the independent variable depending on the physical circumstances. Therefore the mathematical considerations must be more specific and besides the relation $T = bX$ it is also true for this problem that

$$X = b^1T$$

$$\text{and } b^1 = \frac{(1/n)\ \Sigma XT}{(1/n)\ \Sigma T^2}$$

If the standard deviations (σ) are considered

$$\sigma_X = \sqrt{\frac{\Sigma X^2}{n}} \text{ and } \sigma_T = \sqrt{\frac{\Sigma T^2}{n}}$$

and
$$b = r\frac{\sigma_T}{\sigma_X},\ b^1 = r\frac{\sigma_X}{\sigma_T}$$

b and b^1 are the *regression coefficients* and the *regression* equations are

$$T = r\frac{\sigma_T}{\sigma_X}X$$

$$\text{and } X = r\frac{\sigma_X}{\sigma_T}T.$$

The two regression equations mentioned above are represented in Figure 1 by the two straight lines. The smaller the angle between the two regression lines the higher is the degree of association and the greater is the value of the correlation coefficient r. If $r = \pm 1$ the two regression lines concide while if $r = 0$ one line is identical with the X-axis ($T = 0$) and the other with the Y-axis ($X = 0$). The correlation coefficient between air temperature and pool temperature is high. From Figure 1 the small angle between the regression lines verifies the strong association. The combination of the regression equations with dot charts in Figures 1-3 provides additional means of evaluating the relationships between pairs of factors in nature that do not meet the rigorous test of 6 times the probable error.

Effects of Meteorological Conditions on Environment of the Mosquito

Factors

Any useful method for predicting the period of mosquito development on the basis of meteorological conditions is practical only if it depends on weather factors that are normally recorded at weather stations. The thermal condition of a pool is dependent largely on meteorological phenomena; but it is influenced considerably by edaphic factors as well. The probability of estimating the period of mosquito development so far as it is related to thermal conditions of the environment depends theoretically on (i) the degree to which the environment is affected by meteorological conditions and (ii) the accuracy with which the meteorological conditions can be predicted or recorded.

Edaphic factors cannot be neglected in the study of mosquito development, especially when rates of development are compared for different geographical areas. The effects of meteorological phenomena are regulated continually by subsoil temperatures to a degree that varies with elevation and geographical location. Subsoil temperature normally fluctuates from season to season. Although it fluctuates between summer and winter in permafrost areas, the daily variation during late spring and early summer is minimal and almost negligible. The quasi-constant nature of subsoil temperatures during the period of mosquito development in the study area obviated their inclusion among the variables that normally influence the thermal condition of pools.

At least four meteorological factors were considered to have measurable effects on the environment of immature mosquitoes, *i.e.*, air temperature, wind, solar radiation, and precipitation. Rainfall has been described as a limiting factor for mosquito prevalence in temperate and subtropical areas by Headlee (1929, 1930). Mosquito development in subarctic muskeg with subjacent permafrost is rarely restricted by insufficient water in breeding pools. The correlations in the Churchill area were confined therefore to three factors: air temperature, wind chill, and daily sunshine.

(I) *Air temperature.* Air temperature is recorded at weather stations with various degrees of detail. All weather offices customarily record the daily mean temperature; but the reliability of the stated mean varies according to the number of daily readings upon which it is based. For purposes of this study the maximum and minimum air temperatures were used in correlations between pool temperature and meteorological conditions. The daily averages of the maximum and minimum air temperatures were correlated with the daily average one-inch temperatures of the water in eight mosquito pools of various sizes and depths for 45 consecutive days during a normal[6] period of mosquito development. This procedure provided 360 pool temperatures for correlation with air temperature over the 45-day period. The regressions for this correlation are shown in combination with the dot chart in Figure 1. The coefficient of correlation between temperature of the pools and air temperatures was 0.872, with a probable error of ± .079.

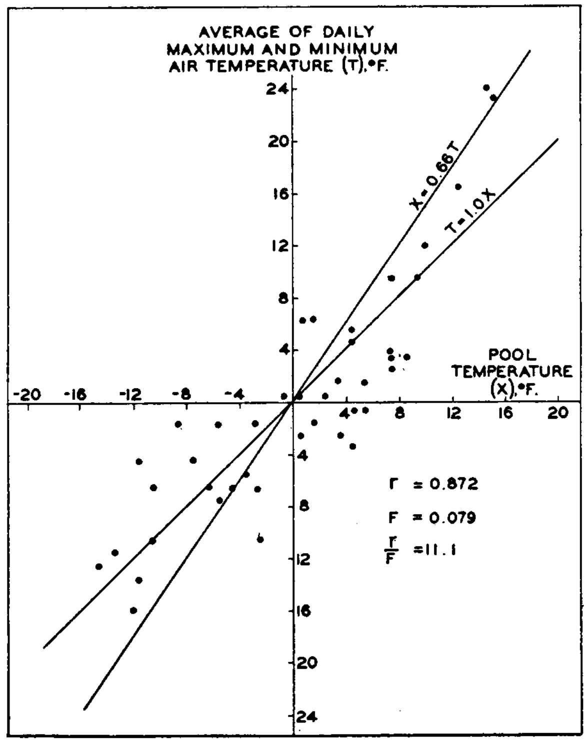

FIG. 1. The daily mean temperatures in degrees F from the seasonal means of (i) the average of the maximum and minimum daily air temperatures and (ii) pool temperature at Churchill, Manitoba, 1952. Each dot represents the average of eight daily mean temperatures, each of which was recorded from one of eight mosquito pools under observation. Coefficient of correlation = r and its probable error = F.

The coefficient of correlation was based on the relation between the average daily temperature of eight pools and the average of the daily maximum and minimum air temperatures. The possibility that the relation depends on several physical phenomena such as conduction, radiation, absorption, and convection of heat was recognized throughout the study. The comparative importance of these physical factors in the transfer of heat between the surface of the earth and the

[6] In this paper, the term "normal" means the average for a season, weather, meteorological element, etc., on the basis of the period covered by weather records for Churchill, *i.e.*, 20 years or more.

lower layers of the atmosphere is still largely unknown on a quantitative basis for biological environments. Therefore the possible influence of empirical classifications of the temperature data on the true coefficient of correlation was also considered. The effect of arbitrary manipulation of weather data on the true relation between air and pool temperatures was tested by varying the treatment of the same data on air temperatures. Three coefficients of correlation (r', r'', r''') were obtained on the basis of three classifications of air temperature over the same period as follows: (i) an average of the maximum and minimum of the current day (r'), (ii) a daily mean of the two-hourly recordings during the current day ending at midnight (r'') and (iii) an average of the daily means of two-hourly recordings during both the previous and the current day ending at mid-night (r'''). Differences between various pairs of these three coefficients of correlation were tested by the method of transforming values of r to the z distribution (Fisher 1950). The values of the coefficients and the significance of the differences between pairs of these coefficients are shown in Table I. The first of the three coefficients (0.872) with a probable error of ± 0.079) has the highest ratio of r to 6 times the probable error and indicates a more accurate treatment of the data as compared with the remaining two. Observations indicated that the lapse in pool temperature in relation to falling air temperature depended considerably on the thermal condition of the banks surrounding the pool, *i.e.*, pool temperature rose more quickly and fell less quickly on the second day of a warm, sunny period than on the first, and similarly on the third as compared with the second. The rhythmic warming and cooling of pool water with the daily rise and fall of air temperature is variable. The maximum pool temperature was reached at various times about 1500 hr in the afternoon and the minimum was reached at various times about 0200 to 0400 hr in the morning. Apparently variations in the times that pool temperature reached the maxima and minima depended on the weather conditions that increased or decreased the influence of one or more of the several physical means of heat exchange such as conduction, radiation, absorption and convection. The relation of the significance of differences between the coefficients of correlation in Table I to the environmental conditions during the study indicate the importance of selecting the proper treatment of data in preparation for statistical analysis. This is especially true when voluminous records such as weather data are condensed by empirical classification to facilitate correlation methods. The differences r'-r'' and r'''-r'' are significant at the 0.1 and the 1 per cent levels respectively. This is to be expected since the coefficient r'' is based on the mean of two-hourly recordings for each day ending arbitrarily at midnight according to standard practice in weather offices. The mean of temperatures recorded during the day and ending at midnight represents the mean air temperature for the *civil day* rather than that for the *daily oscillation* of air temperature that influences the gradual warming and cooling of pool water. This physical reasoning substantiates the high level of significance of r' on the basis of its probable error. It is probably true that the minimum air temperature for any individual day gives some measure of the thermal condition of the pool banks for the previous day and consequently approximates the daily oscillation of air temperature more closely; this may account for the approximate agreement between r' and r''' and the fact that the difference r'-r''' is not significant. The higher probable error in r''' as compared with that in r' indicates that the average of the maximum and the minimum is the most accurate classification of air temperature of the three treatments tested for influence on pool temperature. The maximum and minimum air temperatures are not only easily recorded but they are also to be preferred on the basis of their common use in weather offices.

TABLE I. Coefficients of correlation for the relation between air temperature and the average daily temperature of eight pools and the significance of intraclass differences between paired coefficients based on three classifications of the same air-temperature data.

		Level of Significance of Difference Shown by the t Value for Transformed Values in the Z Distribution	
Classification used for air-temperature data	Coefficient of correlation (r) with probable error in parentheses	Difference between values of Z* corresponding to r	Level of significance† of the difference on the basis of t values
Average of maximum and minimum of the current day	$r' = 0.872(\pm 0.079)$	$Z' - Z''$ $Z' - Z'''$	$< .001$ $> .50$
Daily mean of two-hourly recordings during the current day	$r'' = 0.771(\pm 0.087)$	$Z'' - Z'$ $Z'' - Z'''$	$< .001$ $< .01$
Average of the daily means of the previous and the current day	$r''' = 0.879(\pm 0.091)$	$Z''' - Z'$ $Z''' - Z''$	$> .50$ $< .01$

*Coefficients of correlation r treated by the transformation $Z = \frac{1}{2}[\log_e(1+r) - \log_e(1-r)]$.
†Student's t test.

(II) *Wind chill.* Wind chill is a measurement of the cooling power of the atmosphere on the basis of wind speed and temperature. Cooling power of dry atmosphere has been described by Siple and Passel (1945), particularly at the lower temperatures. Wind chill based on dry air has been recorded continuously at the Churchill weather station in recent years in kg-cal/m^2/hr. The daily average wind chill was correlated with pool temperature for the 45-day period used for correlations of pool temperature with air temperature. The coefficient of correlation between variations in pool temperature and those in wind chill was -0.735, with a probable error of ± 0.048 (Fig. 2). This coefficient is significant on the basis of the magnitude of its probable error. When the correlation between pool temperatures and wind chill was obtained for constant periods of daily sunshine, the coefficient ($r_{XZ.Y}$) dropped to -0.655, with a probable error of ± 0.043.

Theoretically, the computations of wind chill used in these calculations are not exact for all conditions. The thermal conductivity of air increases with an increase in its moisture content. The average moisture content of air in the Churchill region is usually low, justifying the use of dry atmospheric cooling values for most of the year; but during late spring and early summer, when absolute humidity is somewhat higher, the values for wind chill calculated on a dry air basis are probably below the true values. As stated by Siple and Passel (1945), the computation of wind chill may also be subject to errors caused by radiation and thermal convection. From physical principles, the computation of wind chill was probably slightly low for (1) atmosphere of high moisture content, (2) high degrees of convection, and (3) low wind velocities, and by the same token was too high for completely stable and calm air conditions.

(III) *Solar radiation.* Solar radiation is the principal factor in the variations of temperature in different portions of even small shallow pools in the north (Haufe, to be published, a). Normally at most weather stations it has been recorded as the numbers of hours of sunshine per day. This

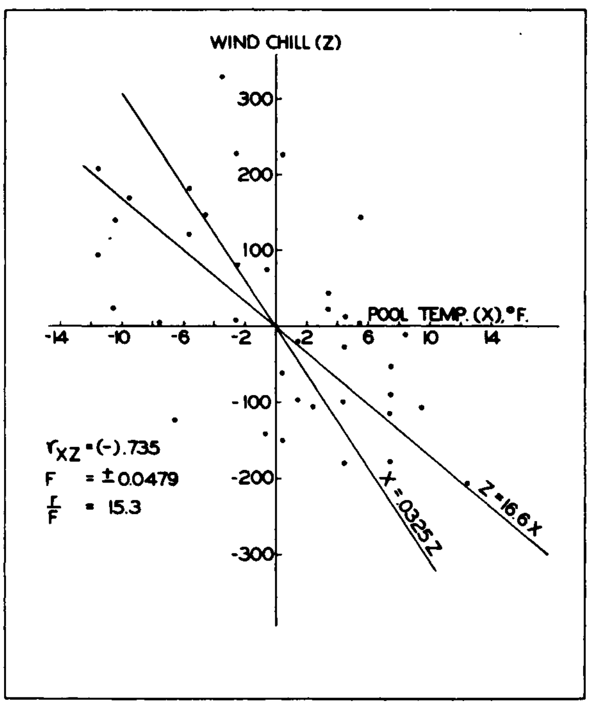

FIG. 2. The daily mean departures from the seasonal means of (i) cooling power of dry atmosphere (wind chill) in kg.-cal./m^2/hr and (ii) pool temperature in degrees F at Churchill, Manitoba, 1952. Each dot represents the daily average of eight mean temperatures, each of which was recorded from one of eight mosquito pools under observation. Coefficient of correlation = r and its probable error = F.

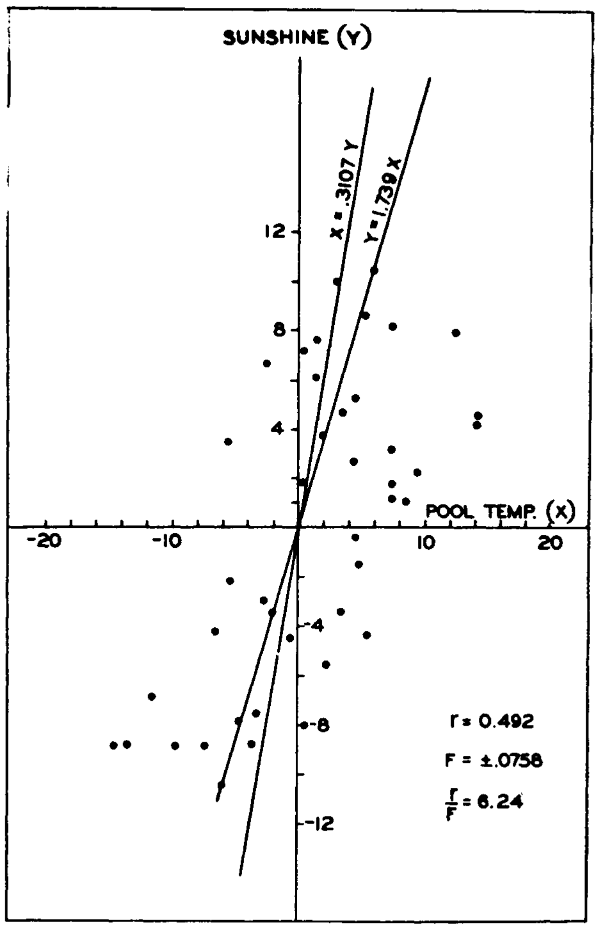

FIG. 3. The daily mean departures from the seasonal means of (i) sunshine in hours and (ii) pool temperature in degrees F at Fort Churchill, Manitoba, 1952. Each dot represents the daily average of eight daily mean temperatures, each of which was recorded from one of eight mosquito pools under observation. Coefficient of correlation = r and its probable error = F.

type of data is inadequate for a quantitative analysis of the effect of solar radiation on mosquito environment since basing solar radiation on daily periods of sunshine arbitrarily presupposes that intensity of solar radiation, and hence insolation of a pool, remains constant throughout the day. Appreciable amounts of solar radiation are detectable even on days with complete cloud cover.

Since recordings by an actinograph were not available at Fort Churchill for this particular study, the correlation was based on the usual sunshine data. The relation between the average daily pool temperatures and daily periods of sunshine for the 45-day period of study is shown in Figure 3. The coefficient between the two variables was 0.492, with a probable error of ±0.076. A value of 6.24 for the ratio of the coefficient to its probable error suggests that there is correlation under the rigorous standards required to distinguish the principal meteorological factors that influence mosquito environment. Other studies (Haufe, to be published, a) suggest that the value of the coefficient was reduced through the use of inadequately quantitative data for solar radiation.

(IV) *Other factors.* At least two factors can be cited as qualifying influences on the regulation of pool temperatures by the principal meteorological factors. Rainfall changes the pool temperature by adding water of a temperature different from that in the pool. During the passage of cold-weather fronts, falling rain may be warmer than the air temperature, and, depending on the time of season, cooler or warmer than pool temperatures. It is not possible to predict corrections for this type of condition; but approximations in temperature correction may be made after the event when the course of pool temperatures is being followed on the basis of calculations from meteorological records. This point will be more adequately discussed in a later section. Air-mass circulation also qualifies the effect of other meteorological factors as a result of certain cloud conditions which are associated usually with general patterns of circulation over a continent. Cloud conditions influence considerably the effect of solar radiation on the temperature of mosquito pools.

Relation of Pool Temperature to Meteorological Conditions

The purpose of all correlations between meteorological factors and pool temperature was to analyze the quantitative effect of a natural combination of the most influential factors such as air temperature, wind chill, and solar radiation on the temperature of environments of immature mosquitoes. The average daily thermal effect of meteorological conditions on the temperature of water in mosquito pools was computed according to a formula based on the coefficients for individual meteorological factors. The weighted average daily thermal effect of meteorological conditions (S) for any 24-hour period was based on the number of degrees by which the minimum daily air temperature exceeded 32° F (T_1), the number of degrees by which the maximum daily air temperature exceeded 32° F (T_2), the wind chill (dry cooling power of the atmosphere) in kg-cal/m²/hr (Z), and the daily amount of sunshine measured in hr (Y). The expression that fits the correlation data best is of the form

$$S = \frac{(T_1 + T_2)\ \sqrt{Y + 1}}{2Z} \qquad \text{(I)}$$

where $\frac{T_1 + T_2}{2}$ represents air temperature.

This expression is based on independent reasoning from physical principles of gain and loss of heat by a body. Although the three principal environmental factors that combine to give S are reliably based on rigorous statistical tests it is also recognized that these factors are probably influenced by lesser factors that contribute to variations under natural conditions. The variability of the ratio of temperature at one inch below the surface in pools to each of the three factors air temperature, radiation, and wind chill was calculated as a prerequisite to the proper weighting of a formula. When each factor was evaluated from data of two seasons subject to influence from the remainder of the environmental conditions the coefficient of variability for this ratio was 32 per cent for air temperature, 50 per cent for wind chill and 49 per cent for solar radiation. The relation of pool temperature to air temperature is less variable since the air temperature is largely dependent on large masses of stable air. Theoretically, the temperature of the surface of the terrain and static pools should follow that of the lower layer of the air mass with varying amounts of lag depending on the influence of other factors. Radiation and wind chill may be considered to oppose each other in the modification of effects of air temperature on pools. Since the coefficients of variability are approximately equal for wind chill and radiation there is no necessity to weight them further in the expression for S. The relation between wind chill and pool temperature is rectilinear but the effect of radiation on pool temperature is curvilinear. Dulong and Petit (Stewart and Satterly 1946) made a laborious investigation of the variation of emissive power of a radiating surface in relation to the temperature of surrounding media. They expressed the relation as follows: "For a given excess of temperature the rate of cooling increases in geometrical progression as the temperature of the enclosure increases in arithmetical progression." The net gain of temperature in a pool from radiation therefore decreases for a given intensity of sunlight as the temperature of the pool rises in relation to the air temperature. For example, cold pool water warms up quickly in early morning under radiation when the temperature differential between the pool and warmer air is large; but in the afternoon the rate of warming from radiation decreases as the pool temperature approaches the air temperature and a larger proportion of heat is emitted from the pool through outgoing as compared to incoming radiation. This general relation is verified from correlation data when Y to the power $\frac{1}{2}$ is used in the expression for S. For practical purposes the value of S cannot equal zero on a day when radiation in hours of sunshine is recorded as zero. If $\sqrt{Y+1}$ is used instead of $\sqrt{Y}$ the formula applies to overcast as well as sunny days.

Points showing the relation between the average daily thermal effect of meteorogical conditions (S) and the daily average of one-inch pool temperature (X) are plotted in Figure 4. The points represent 45 consecutive days in which weather was extremely variable with precipitation on all but 14 days. The circles represent days in which there was sufficient precipitation to raise the water level in the pools under study. The crosses represent days that were hazy or partially overcast with warm temperatures and exceptionally high absolute humidity. The effects of heavy precipitation and inadequate quantitative data for solar radiation are obvious.

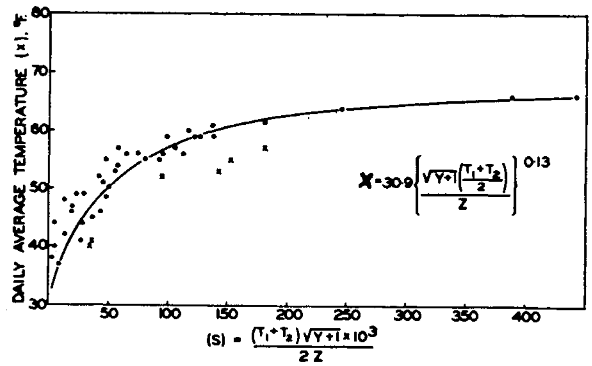

FIG. 4. The average daily thermal effect of meteorological conditions (S) and the daily average pool temperature (X) in degrees F for eight pools. Dots represent days with little or no cloudiness; crosses, the days with haze and exceptionally high absolute humidity but no rain; circles, the days with heavy overcast and sufficient precipitation to raise water levels in static pools.

The data recorded for the 14 days that had no precipitation during daylight hours and insufficient amounts during darkness to change the water levels in pools are summarized in Table II. When log X is plotted against log S for the values in Table II the relation is that of a straight line as shown by the dots in Figure 5. The equation describing the relation is therefore of the form $X = a\ S^n$. It follows then that the particular smoothed parabola may be plotted to represent the relation between X and S by subjecting most-representative pairs of points to the relation

TABLE II. Weighted average daily effects of meteorological conditions (S) on pools for 14 days not characterized by heavy overcast or precipitation

Date (1952)	Average of mean pool temp. °F (X)	Minimum daily air temp. °F	T*	Maximum daily air temp. °F	T*	Daily average wind chill kg-cal/ m^2/hr (Z)	Daily sunshine hr (Y)	$\frac{(T_1+T_2)\sqrt{Y+1}}{2Z}$ (S)
VI-30	66.0	57	25	84	52	330	13.0	.443
VI-29	65.5	58	26	84	52	384	13.4	.388
VI-28	64.0	46	14	79	47	422	16.7	.302
VII-7	60.0	41	9	62	30	600	14.1	.137
VI-22	59.0	40	8	55	23	537	16.9	.126
VI-23	57.0	42	10	52	20	631	17.4	.102
VI-24	56.0	40	8	52	20	526	11.5	.095
VI-20	55.0	40	8	57	25	639	13.5	.092
VI-17	53.0	32	0	58	26	618	14.9	.084
VI-19	51.0	39	7	56	24	703	4.4	.053
VI-14	48.5	35	3	53	21	719	5.9	.044
VI-12	44.0	32	0	51	19	633	16.7	.034
VI-7	42.0	40	8	58	26	779	0.0	.021
VI-8	37.0	33	1	44	12	998	0.0	.007

*The number of degrees by which the minimum or maximum air temperature exceeded 32° F.

$$\log S - \log S_1 = \frac{\log S_2 - \log S_1}{\log X_2 - \log X_1}(\log X - \log X_1). \quad \text{(II)}$$

Comparison of various curves with the trend of the point cloud in Figure 4 showed that the particular relation between X and S is fitted best by the parabola

$$X = 30.9 \left\{ \frac{\sqrt{Y+1}\left(\frac{T_1 + T_2}{2}\right)}{Z} \right\}^{0.13} \quad \text{(III)}$$

For practical purposes within the degree of variability experienced the formula can be simplified to the form

$$X = 31 \left\{ \frac{\sqrt{Y+1}\left(\frac{T_1 + T_2}{2}\right)}{Z} \right\}^{1/8} \quad \text{(IV)}$$

A mathematical check for the conformity of the simplified form of the equation to the point cloud is shown in Figure 5. The crosses represent values of X calculated by means of equation IV and they obviously fit the original straight line more closely than the dots.

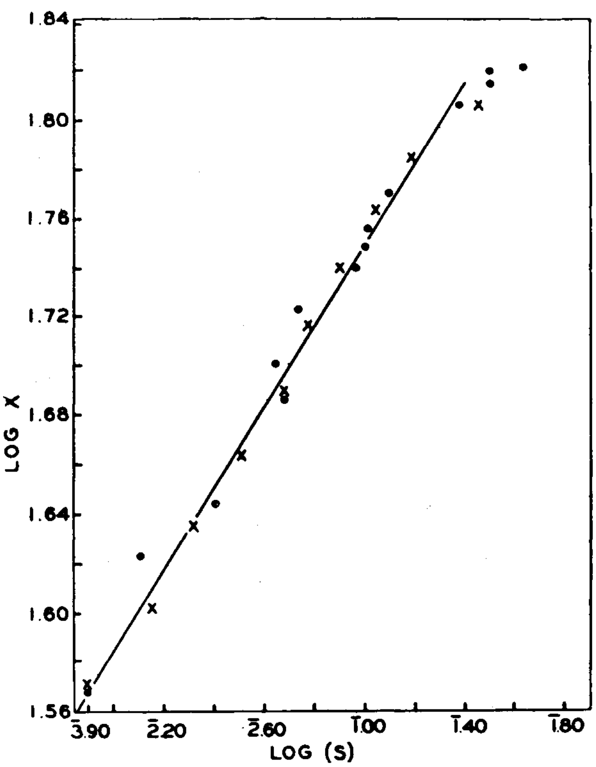

FIG. 5. Agreement of (i) values taken from field records (dots) and (ii) values based on the established equation IV (crosses) in the relation between pool temperature (X) and average daily thermal effect of meteorological conditions (S).

The discrepancies shown by the values represented by crosses and circles in Figure 4 are probably explained by the weather conditions recorded for those days. The crosses represent the comparatively few days when the general circulation was from the south to southeast. This type of circulation produced warm, humid air conditions as compared to the warm, dry air conditions associated with the more prevailing south to west circulations. The calculated daily thermal effect of meteorological conditions was undoubtedly high on those six days since the method of measurement of cooling power of the atmosphere disregarded the high rate of thermal conductivity due to the excepitonally high moisture content of the air. Haze was usually associated with south to southeasterly circulation. Quantitative recordings by an actinograph would undoubtedy show a proportionately lower rate of insolation than recordings based on hours of sunshine. This circumstance would also partially contribute to the high value of S on these days. The departure of the values represented by circles from the smoothed curve are probably associated with cloudy conditions before and after the periods of precipitation that were recorded on these days. Even with complete overcast on days when no sunshine was recorded by the usual method, spot recordings of solar radiation by a photoelectric heat radiation meter were obtained up to 0.55 g.-cal./cm^2/min. High pool temperatures also may have been partially due to the addition of precipitation that was warmer than the original pool temperature. However, consistently high pool temperatures on rainy days during the passage of both warm and cold weather fronts indicate that inadequate records of lower amounts of solar radiation were mainly responsible for the low calculated values of S.

THERMAL CONDITIONS OF ENVIRONMENT

"Time x temperature" Components

Concepts of developmental rates in life-cycles of insects have generally been described on the basis of the two parameters, time and temperature. Several thermometabolic curves have been constructed to approximate the velocity of development either for various stages or for the whole development of an organism. The views of Bodenheimer (1927), Bodine (1925), Crozier *et al.* (1926), Krogh (1914), Peairs (1927), Pearl (1927), Sanderson and Peairs (1917) and others are possibly resolved into four principal theories as to the nature of the velocity curve. Some of the viewpoints have been determined by laboratory investigations; others are the result of field investigations on various arthropods. A number of workers, notably Bodine (1925), Cook (1927), and Parker (1930), have shown that variable temperature has an accelerating effect upon insect metabolism. Developmental rates for mosquitoes may be higher under natural conditions with variable temperature than in a laboratory at comparable constant temperatures.

In earlier investigations at Fort Churchill by Hocking *et al.* (1950) the "degree-day" with an empirical lower threshold of 32° F for air temperature was suggested as a suitable "time x temperature" component to describe the period of development of northern *Aedes* mosquitoes. The detailed studies described in this paper on the biology of *Aedes* mosquitoes in the same area indicated that the lower threshold of development of individual species must also be considered when these parameters are used.

The development of *A. communis* was studied in detail during one season. The results of this investigation are tabulated in Table III. The temperatures shown are based on the average one-inch temperatures of the pools during the period of development of the mosquitoes: the one-inch pool temperatures were corrected for effectiveness on mosquito development from curves that represent the daily vertical displacement of larvae in a pool in relation to temperature gradients in the water (Haufe, to be published, a). As explained in the paper just mentioned, there is extreme variation of temperature within a pool. Mosquito larvae select temperatures both horizontally and vertically. Both displacements are important in the tabulation of pool temperatures that affect the development of mosquitoes; but only one, the vertical displacement, can be usefully employed in estimating the actual temperature that directly influences development. For instance at Fort Churchill, *A. communs* usually selects the surface layer of water until the surface temperature rises beyond 62° F. Thereafter larvae aggregate at lower levels, except for occasional sorties to the surface. *A. communis* has a temperature preferendum of approxiamtely 61° F based on field studies. This behavior pattern was incorporated in the method of estimating pool temperatures that correspond to the development of mosquitoes. The recorded average one-inch temperature of a pool was the average of half-hourly temperatures for the day taken from a continuously recording thermometer. Therefore all half-hourly temperatures above 61° F were reduced to 61° F in the calculation of daily "effective" one-inch temperatures that were related to mosquito development. The temperature to which larvae were theoretically subjected on the basis of these corrections is designated as the "effective pool temperature" in further discussion.

When the period of development was plotted against the average effective pool temperature, the curve could be described as an equilateral hyperbola at least for the range of temperatures found in the area under natural conditions. The general equation of the curve representing the relation of mosquito development to parameters of time and temperature is of the form

$$D\ (t - C) = K, \qquad \text{(V)}$$

where D is the period of development, t is the average effective environmental temperature, C is the lower threshold of development for the species, and K is a thermal constant in units of "time x temperature."

The curves of development for *A. communis* under natural conditions are shown in Figure 6. The equations comparing the development of males and females indicate that the lower threshold of development for both sexes in natural

TABLE III. Periods of development of males and females of *A. communis* at various average "effective" environmental temperatures

Pool	Males		Females	
	"Effective" environmental temperature °F (t)	Developmental period, days (D)	"Effective" environmental temperature °F (t)	Developmental period, days (D)
A (1951).....	45.5	36	46.0	39
B (1951).....	46.7	33	46.6	36
W (1952).....	46.9	28	47.8	33
X (1952).....	47.4	24	48.5	29
V (1952).....	49.9	23	50.4	25
Y (1952).....	52.9	18	51.9	23
Z (1952).....	No emergence		53.3	20

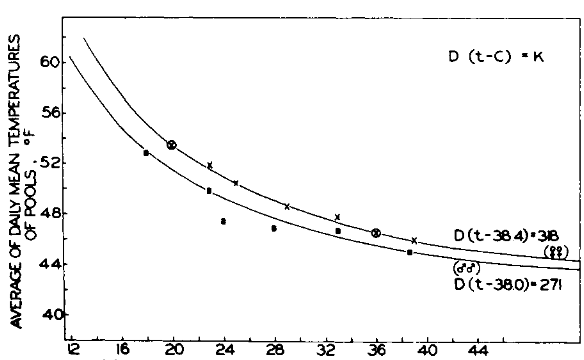

FIG. 6. Average daily mean "effective" environmental temperatures and periods of development of males (squares) and females (crosses) of *A. communis*. "Effective" environmental temperature (t) is temperature that is corrected on the basis of behavior patterns of mosquitoes in a pool and does not correspond exactly to absolute pool temperature (X) (see text).

pools was approxiamtely 38° F; but the thermal constant for females was 318 degree-days as compared to 271 for males. The lower thermal constant is a direct consequence of the three-day period by which the peak emergence of males precedes that of females. The equilateral hyperbolae in Figure 6 were drawn to satisfy two extreme values obtained for the period of development of each of the sexes, *i.e.,* those in pools A and Y for males, and those in B and Z for females as tabulated in Table III. The values from other pools were plotted on the same graph to indicate the degree of agreement between periods of development that are described by the hyperbolic relation based on the parameters time and temperature. The curves were not produced to apply to pool temperatures above 62° F since studies on the behavior of *A. communis* under natural conditions showed that the species did not select temperatures above 62° F for its environment if there were vertical or horizontal temperature gradients in the pool (Haufe, to be published, a).

Comparison of Species in Rates of Development

The periods of development of pest species of mosquitoes at Fort Churchill were compared during the summer of 1952 in at least three pools for each species. Curves describing rate of development were constructed from the two extreme values obtained for each species. The remaining value (or values), as described previously for *A. communis,* provided a check on the reliability of each specific curve. It was assumed that the equilateral hyperbola was valid in describing the development of other mosqutio species over the range of pool temperatures experienced under natural conditions. Observations of the behavior of larvae of *A. impiger, A. punctor,* and *A. nigripes* indicated that their temperature preferenda were approximately the same as that of *A. communis.* Temperature preferenda apparently were below 61° F for *A. impiger* and *A. nigripes* and below 63° F for *A. punctor.* Other species such as *A. excrucians, A. hexodontus, A. pionips, A. campestris,* and *A. flavescens* showed indications of preferring higher temperatures on occasion; therefore the one-inch temperatures, irrespective of magnitude, were considered to be the effective developmental temperatures of these species.

The hyperbolic curves constructed from data on the development of six species of *Aedes* mosquitoes are shown in Figure 7. The curves indicate that the lower thresholds of development of the larger species, *i.e. A. excrucians, A. pionips,* and *A. hexodontus,* are higher than those of the smaller species, *i.e. A. communis, A. punctor,* and *A. impiger,* The larger species except *A. hexodontus* appear to have the larger thermal constants. In studies on the behavior of adult mosquitoes (Haufe, to be published, b), populations of *A. hexodontus* usually reached their peaks more abruptly than those of any other species in the same area. The normally short period of emergence for a seasonal brood is associated with the comparatively low thermal constant for this species. This suggestion is in agreement with observations on the associations between *A. punctor* and *A. hexodontus* in field pools in the same locality in each of three successive years. Although often associated with *A. punctor* in the same pool, *A. hexodontus* was not observed to appear in the pool as early in the season as the former. However, the period between the appearances of *A. punctor* and *A. hexodontus* adults was generally shorter and was certainly never longer than that between the appearances of *A. punctor* and *A. hexodontus* larvae in the same pool.

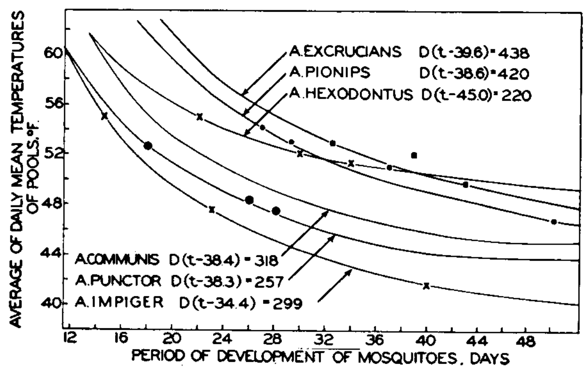

FIG. 7. Equilateral hyperbolae describing periods of development in relation to "effective" environmental temperature of the females of six common species of *Aedes* mosquitos at Fort Churchill, Manitoba.

The thermal constants and lower thresholds of development for the common species of *Aedes* at Fort Churchill are tabulated in Table IV. *A. nigripes* did not breed in the area selected for the study. Observations on open tundra indicated that this species had approximately the same lower threshold of development as *A. impiger,* but probably had a slightly higher thermal constant. *A. impiger* and *A. nigripes* larvae appeared about the same time in pools, but the adults of *A. impiger* preceded slightly those of *A. nigripes* in order of appearance in flight and attraction to man. *A. flavescens* might be expected to have a developmental curve approximating that of *A. excrucians.* These two species appeared as larvae in pools and were observed for the first time as adults on approximately the same date each season. *A. campestris* probably parallels *A. excrucians* most closely in its development. *A*

TABLE IV. Thermal constants and lower thresholds of development of *Aedes* mosquitoes at Fort Churchill, Manitoba

Species	Thermal constant (°F x days)	Lower threshold of development °F
Females		
A. impiger (Walk.) *......	300	34
A. nigripes (Zett.) *.......	300	34
A. punctor (Kirby) *......	260	38
A. communis (Deg.) †.....	320	38
A. hexodontus Dyar *......	220	45
A. picnips Dyar ‡.........	420	39
A. excrucians (Walk.) *....	440	40
A. flavescens (Muller) ‡....	440‡	40‡
A. campestris D. & K. ‡...	320‡	38‡
A. cinereus Mg. ‡.........	260	38
Males		
A. communis (Deg.).......	270	38

*Posing a serious problem through abundance and intense biting.
†Causing slight or no nuisance to man.
‡In moderate numbers or exhibiting moderate biting activity, or both.
‡By inference from field observations on order of succession of and association with the various species throughout the mosquito season for 3 consectuive seasons.

cinereus was associated with *A. punctor* in one of the pools under observation. *A. cinereus* adults emerged 1 to 2 days after *A. punctor* and the species probably have nearly similar thermal constants.

Relation of Topography to Development

The topography of some areas probably influences the development of mosquitoes to considerable degrees depending on the effect of physiographical features on the climate. Mosquito development was delayed very little in large deep pools as compared to small shallow pools. The studies on behavior of immature mosquitoes had shown that larval activity was restricted usually to warm, shallow peripheral portions of pools larger than normal. For this reason it is probable that mosquitoes that develop in large pools are subject to effective environmental temperatures that closely approximate those of smaller pools.

In the level muskeg common to terrain in the Fort Churchil alrea (Fig. 8) topographical features had little effect on the uniformity of emergence of mosquito populations except where large snow drifts covered pools late in the season. Significant variations in emergence of adult populations were associated with greater density of shrub and particularly of forest cover. Observations on populations with mixed species indicated that the time from beginning to end of mosquito emergence was 4 to 5 days in tundra pools as compared to 6 to 10 days in woodland pools. Observations on populations containing a single species, *A. communis,* showed that the time from the beginning to the end of emergence of the adult females was approximately 4 to 5 days in pools exposed completely to the free play of meteorological elements, 5 to 6 days in pools surrounded by low shrub, and 8 to 10 days in pools closely bordered by spruce trees. The periods for the complete emergence of both sexes were 2 to 4 days longer in each category because the emergence of males preceded that of females by approximately that period under natural conditions. In large pools with highly irregular contours, vegetative cover along the banks may interfere with the effects of meteorological elements on the pools so that complex patterns of behavior may develop within a population of mosquitoes. The influence of environmental factors may be so complex that a population of a single species is divided into groups isolated from each other by unfavorable environmental conditions throughout most or all of their period of development. A general survey in 1950 within the transition belt between forest and tundra was designed to give approximate figures on the variation of emergence in different localities. A large number of pools were sampled systematically at daily intervals to recover fourth instar larvae of *A. communis.* The pools represented a series on level mossy plain progressing from the shallow, regular-bordered, barren type of pool to the irregular-bordered, deep type found in small stands of scrub spruce. Six pools were sampled at each station and fourteen stations were included in the series between the two extremes of vegetative cover. The variation of the time marking the last capture of fourth instar larvae was 3 to 5 days or almost 20 per cent of the average period of development at each station for pools on barren plain as compared with 6 to 10 days or 41 per cent of the developmental period at each station within stands of scrub spruce. Assuming that these variations in rate of development of larvae are reflected in the variations of periods of emergence of adults, the abundance of adults is less predictable in wooded areas with irregular pool conditions than in the tundra. Mosquitoes apparently select specific breeding places (Haufe 1952; Horsfall and Morris 1952). This tendency may eliminate much of the variation in rate of development of mosquitoes caused by topographical influences that are associated with various types of vegetative growth.

Variation of Temperature between Pools

The accuracy of formulae suggested for the prediction of mosquito emregence depends largely on the degree of variation in temperature to be expected between pools. We stated above that pools selected for correlations represented a wide varia-

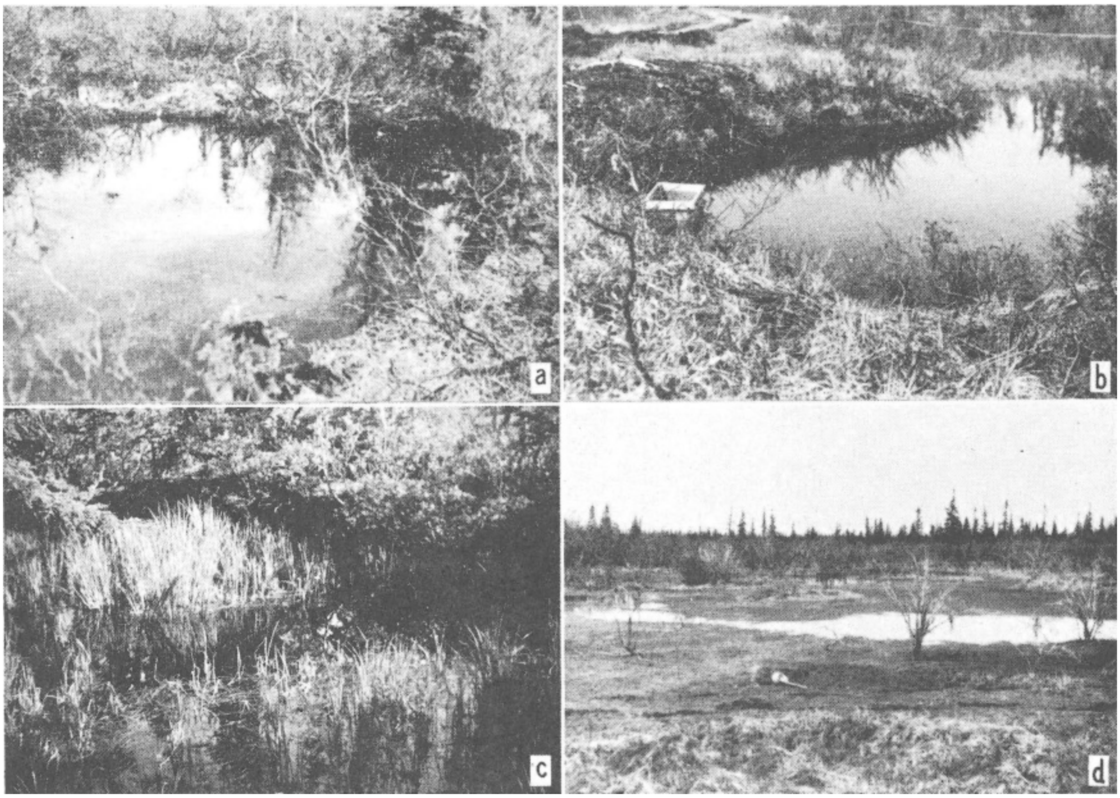

FIG. 8. Pools typical of the study area, in transition between tundra and Boreal forest. a and b, Deep, permanent type with steep banks in scrub-willow muskeg. c, Quasi-permanent, grassy type of shallow pool in scrub-spruce forest. d, Shallow, flood-plain type near water course with muck bottom.

tion in size and in proximity to vegetative cover. A comparison of mean daily temperatures at a depth of one inch is presented in Table V for six pools. The pools listed in the table were classified as follows: *V*, *W* and *X* were small, average and large pools respectively with no vegetative cover to influence the effects of either solar radiation or wind. *X*, *Z*, and *X-1* were all averaged-sized pools; but their vegetative cover was characterized by tall grass, scrub willows and scrub spruce respectively. The last-mentioned pool represented a very small proportion of the pools usually found in tundra or tundra-forest transition. It was also the last pool to show open water in the spring since it was beneath a large snow drift in a small island of scrub spruce. The period shown in the table, June 11 to July 2, 1952, does not represent the periods of development of mosquitoes in respective pools but rather the period beginning with the disappearance of surface ice from *X-1* and the drying up of *V*. The emergence of mosquitoes was almost completed in pool *V* by the time water disappeared. The six pools were selected at intervals of approximately a week as open water appeared. They were primarily designed to provide a series of "time-temperature" products in rela-

TABLE V. Variation of mean surface temperatures among pools representing a wide range of size and vegetative cover at Fort Churchill, Manitoba, in 1952

Date	MEAN POOL TEMPERATURE (°F)						Maximum deviation
	V	*W*	*X*	*Y*	*Z*	*X-1*	
June 11....	46.0	46.5	46.0	45.5	49.0	46.0	±2.5
12....	49.2	48.5	47.5	45.5	46.0	47.0	±2.2
13....	47.6	48.0	47.0	46.0	46.5	46.0	±1.2
14....	52.0	50.0	50.0	49.0	48.5	48.0	±2.4
15....	49.2	50.0	49.0	48.5	49.0	47.0	±1.8
16....	51.2	50.5	50.5	50.5	50.0	50.5	±0.6
17....	53.5	54.0	53.0	53.5	51.5	52.5	±1.5
18....	56.5	58.5	57.0	56.7	56.5	57.0	±1.2
19....	54.7*	50.5	50.0	51.5	49.0	48.5	±4.0
20....	55.2	54.5	54.5	54.0	55.5	54.5	±0.8
21....	61.2	60.5	60.0	58.5	61.5	59.5	±1.7
22....	62.0	60.0	60.2	59.0	61.0	58.5	±1.9
23....	58.0	59.5	58.0	57.0	59.0	57.0	±1.4
24....	58.0	59.0	58.5	57.5	58.0	57.5	±0.9
25....	54.7	56.0	54.5	53.5	55.0	52.5	±1.9
26....	56.0	57.5	56.0	57.5	56.0	54.0	±2.2
27....	63.0	62.0	60.5	61.0	62.0	57.0	±3.9
28....	66.0	65.0	63.0	65.0	65.0	59.0	±4.8
29....	65.5	69.0	65.0	69.0	68.0	62.0	±4.4
30....	68.0	69.0	68.5	70.0	69.0	63.5	±4.3
July 1....	61.2	62.0	60.5	63.5*	59.5	57.0	±3.5
2....	50.0	51.5	50.5	49.5	49.5	49.5	±1.4
Average..	56.3	56.4	55.4	55.5	55.7	53.9	.....

*Pool flooded with surface drainage following heavy precipitation.

tion to mosquito development. Consequently the series of temperatures for pools *V*, *W*, *X* and *Y* represent the environment for the later part of mosquito development while pools *Z* and *X-1* represent a period midway in mosquito development. The variation in temperatures among these pools is perhaps greater therefore than in a random selection of pools showing open water at the time of a general spring thaw. As shown in Table V, the difference in the averages of the temperatures for pools over the period are not significant on a field scale except for pool *X-1* which was specially selected for late development of mosquitoes. The maximum deviation between pools for given days varied between ± 0.6 and ± 4.8°F. Inspection of the deviations shows that they increase as the pool temperatures rise. Behavior studies on *A. communis* (Haufe, to be published, a) have shown that mosquitoes select preferred temperatures along horizontal and vertical temperature gradients and that the preferenda are at approximately 60-62° F. Since the greater deviations of temperature between pools occur above 60° F they are relatively insignificant in affecting the development of mosquitoes that are subjected to the steep temperature gradients that are characteristic of pools at northern latitudes.

Discussion

Prediction of mosquito emergence depends largely on the accuracy of meteorological probabilities. Long-range forecasts show slight promise until appropriate methods have been perfected. Short-range prediction of specific mosquito emergence in northern Canada, however, may be feasible where daily meteorological records representative of the immediate area are available. The thermal effect of meteorological conditions can be additively compiled from day to day to indicate from established thermometabolic curves the expected time of appearance for a given species. The accuracy of this type of prediction would increase progressively day by day from the time of the general appearance of open water at the banks of mosquito pools to the date of general emergence of the adult mosquitoes. Judgment would be required only in the selection of the date that represents the time of general exposure of the banks of pools during the spring thaws.

Blunck (1923) suggested that the equilateral hyperbola might be adapted to describe the development of dry-land insects during the immature stages. Our studies indicate that the equilateral hyperbola is representative of the development of the post-hatching stages of *A. communis* over the range of temperatures normally experienced in pools in permafrost terrain. The use of hyperbolae to describe development under natural conditions requires that the "effective" environmental temperature based on patterns of behavior is a parameter of the "time x temperature" component for any individual species. Although the curves of development for species other than *A. communis* are based on less detailed data than those for *A. communis*, the values obtained for thermal constants and lower thresholds of development agree with the natural succession of species observed during three successive seasons. Values for developments of the various species agreed not only with the natural order of appearance of first-instar larvae in the pools but also with the peak activities of the adults.

The three-year period of study was representative of the extreme variations in meteorological conditions that might normally be expected in the area. The spring season of 1950 was exceptionally cold with monthly mean temperatures as much as 8° F below normal and precipitation above normal. The following year was a normal season for both temperature and rainfall. In 1952 monthly mean temperatures were considerably above normal through March, April, May, and June, and reached a peak of 12° F above normal in May; precipitation in these four months was the heaviest for the three years.

The algebraic expression suggested for the relation between pool temperature and meteorological factors were developed from data for permafrost terrain. Since the effects of permafrost in cooling pool water below air temperatures were quasi-stable during the periods of study and consequently were not expressed in absolute units in the derived equations, the parabolic relation (formula IV) may be restricted to typical permafrost areas. Application of this type of formula to temperate areas would require further research on the relation of seasonal variation in subsoil temperature to the effects of meteorological factors on pool temperature. As compared to permafrost areas, in which the subsoil temperature at a 6-inch depth may remain quasi-constant during late spring and early summer, in temperate climates a gradual seasonal variation is known to exist at the same depth. At lower latitudes variable subsoil temperatures may have a considerable effect on pool temperatures.

Topographical variations would undoubtedly have serious effects on the relation between pool temperatures and meteorological conditions. The Churchill area is flat; except for interference by vegetation, pools were equally and normally exposed to the natural daily succession of meteorological phenomena. In rolling, sloping, or mountainous terrain, pools may be more or less exposed to meteorological conditions characteristic of one part of the day than to those of another part, depending on the disposition of physiographical features. For instance, solar radiation, winds, cloud cover, and precipitation are all seriously influenced by mountain ranges. Schubert (1928) has described in detail the variations in the sum-effects of daily solar radiation associated with various degrees of inclination of insolated surfaces to the path of incident radiation in the region of Potsdam, Germany. From Schubert's data the effects of solar radiation on environmental temperatures in mountainous regions may be expected to be complex. Schade (1917) found that the surface characteristics of treeless terrain varied so much that extreme differences in temperature were recorded within distances as little as 50 metres on ground surfaces exposed to the weather. His detailed records showed that the difference between minima seldom exceeds 2° C; but by day, when incoming radiation is effective, the differences in maxima may be as great as 37° C for two sites at the same distance. Comparison of the effects of meteorological conditions on environments in different geographical regions would require a classification of terrain on the basis of meteorological changes that are associated with certain categories of physiographical features.

These studies indicate the necessity of continuous records as opposed to spot recordings of meteorological elements in ecological studies on mosquitoes. Ecological formulae of the type described in this paper require improvements in the general documentation of weather at meteorological stations. Three improvements that appear to be most important at the present stage of this study are: (i) records of the cooling power of the atmosphere, including thermal conductivity of air, *i.e.*, atmospheric cooling based on moisture content of the air as well wind speed and temperature, (ii) continuous summation of daily solar radiation in absolute units (g-cal/cm^2/min), (iii) more precise values of average wind speeds. In the analysis of the thermal effects of meteorological elements on mosquito pools it was remarkable to find a lower statistical correlation for daily sunshine than for average daily wind chill. It is possible that the inadequacy of the summation of solar radiation on the basis of daily hours of sunshine, as opposed to continuous recordings by actinograph in absolute units, is responsible for this relation in the data. Geiger (1941) has stressed the importance of solar radiation recorded as a daily sum in cal/cm^2 in the analysis of ecological relationships involving micrometeorological elements. This view is supported by the fact that during the studies at Fort Churchill spot recordings of solar radiation of up to 0.55 g-cal/cm^2/min were obtained with a photoelectric heat radiation meter on overcast days on which zero hours of sunshine were recorded.

In addition to its influence on environmental temperatures, solar radiation had significant effects on the patterns of behavior of mosquito larvae (Haufe, to be published, a). The sum effect of solar radiation in promoting the development of mosquito larvae in field pools may still be underestimated. Related field studies on behavior and ecology of mosquitoes (Haufe, to be published, b) have indicated that insects may develop at different rates because they behave differently in nature and that ignorance of this fact may lead to serious error.

When lower thresholds of development were used as a basis for the establishment of thermometabolic curves for mosquitoes under natural conditions, the thermal constants appeared to bear some relation to the size of the insect. The larger species generally had the larger thermal constants. Bodine (1925), Cook (1927), Parker (1930), and others have shown in laboratory experiments that fluctuating temperatures promote higher velocities of development than constant temperatures. The association between body size and thermal constant probably depends on the rate of heating and cooling associated with the ratio of surface area to the volume of the insect. Since the ratio of surface area to unit volume is greater for smaller bodies than for larger bodies, higher rates of heating and cooling should theoretically be associated with the smaller mosquitoes. Where thermal conductivity is limited to water, the greater rate of heat gain of small larvae during rising temperatures should be cancelled approximately by the greater rate of heat loss of small larvae during falling temperature. However, it is probable that mosquito larvae, especially when resting near the surface, absorb some solar radiation directly to increase their body temperatures. The behavior patterns of mosquito larvae under natural conditions during periods of high insolation indicate that this may be true, especially when environmental temperatures are below the preferendum (Haufe, to be published, a). When pool characteristics are such that the larvae can select continually temperatures that do not exceed their preferendum, the relation of surface area to body volume would be an important factor in the ability of larvae to increase body temperature by direct absorption of heat from both solar radiation and pool water.

Some important limitations to the use of the equilateral hyperbola in describing the development of mosquitoes under natural conditions must be recognized. The curve can be expected to be representative of development only over the range of temperatures below or equal to the species preferendum unless the mosquito has freedom to select temperatures that do not exceed its preferendum during the period of development. Usually the development of insects decelerates when the temperature is increased beyond the optimum (*e.g.*, Andersen 1930; Krogh 1914; Larsen and Thomsen 1940). For supraoptimum temperatures the relation between period of development and temperature would depart from the form $D(t-C) = K$. In pools studied in permafrost areas, vertical or horizontal gradients were always sufficient to permit larvae to select optimum and suboptimum temperatures during the period of development. When surface temperatures became exceptionally high in the shallow muddy pools in floodwater muskeg, mosquito larvae were commonly observed to be resting within the loose muck which formed the bottoms of such pools to a depth of several inches above permafrost in the summer. Gradients measured in pools under these circumstances had surface temperatures as high as 80° F, which was considerably in excess of the 61-63° F preferenda of some of the local species. The temperature just below the surface of bottom muck was not observed on any occasion to exceed 58° F in the smallest of pools that had water to a depth of at least two inches. Therefore it is probable that mosquito larvae in permafrost areas develop within environments that rarely, if ever, exceed the temperature preferendum. In temperate and tropical areas this is not likely to be true. The use of equilateral hyperbolae in prediction of mosquito emergence is restricted, therefore, not by geographical areas but rather by the relation of the temperature preferendum of the species to the normal climate. On the North American continent the suggested formulae may be applicable with increasing accuracy progressing north and east of the middle of the geographic distribution of a species and with decreasing accuracy progressing south and west, provided comparisons are made at equal altitudes. In mountainous terrain the same type of formulae would be more representative of development at altitudes above the mean for the vertical distribution of the species where development is subjected to suboptium mean environmental temperatures; at altitudes below the mean for the vertical distribution of a species the development would be subject to supraoptimum mean temperatures unless the character of the pools permitted selection of environments with optium or suboptimum temperatures. These conditions seriously restrict the use of the equilateral hyperbola. Much investigation appears to be necessary to establish the territorial applicability of methods discussed in this paper.

The application of physical formulae to the prediction of mosquito development may be subject to important influences from edaphic and nutritional conditions and population densities. On a local basis these influences may be expected to cause considerable variation in times of emergence by affecting the microenvironment of the immature stages. It is probable that the physical conditions of an environment such as temperature and light are limiting factors in some of the biological processes involved in mosquito development. The ecological aspects of the influence of population density, nutrition, and edaphic factors have been given little, if any, attention in investigations of mosquito biology. Beckel (1953) reported indications in preliminary experiments that temperature may be a limiting factor in the action of a hatching stimulus from decaying organic matter for some of the *Aedes* species of the Churchill area. He found that infusions of decaying mosquito bodies stimulated hatching of the eggs of *A. hexodontus* and *A. campestris* at appropriate temperatures. It is possible that the activity of microorganisms may influence the rate of hatch, especially in species that have a diapause, and thereby contribute to the variation in the developmental period in relation to physical conditions of the environment. Beckel stated that *A. hexodontus* hatched in the laboratory at temperatures slightly above 0° C. In the investigations reported in this paper the lower threshold of development was indicated to be approximately 45° F in nature for the same species. It is noteworthy that the curve did not conform with those of other species with comparable body sizes. Development may have been retarded disproportionately in the lower part as compared to the higher part of the temperature range. This would account for an abnormally high value for the apparent lower threshold of development. If other edaphic hatching stimuli are more vital to the embryonic development of *A. hexodontus* than to co-existent species the lack of these stimuli in the early flood conditions of pools might abnormally retard the general hatching of the eggs. This may cause a serious variation in lower thresholds of development that are calculated from natural emergence. Comparison of times of development and their variation in this paper are confined principally to the black-legged *Aedes* group of mosquitoes that have a diapause that is followed by a single annual brood. Generally speaking from studies on other insects the variations in rate of development are compressed in populations of single-brooded species after a diapause in the egg stage. The black-legged species of *Aedes* that form the greater part of the abundance of mosquitoes at Churchill hatch quickly in the early part of the spring with the first appearance of open water. Moisture is not a limiting factor in the development of the early species of mosquitoes in the transition area between tundra and forest; it is reasonable to expect therefore that the large variations of emergence from irregular pools is a reflection of factors influencing the development of the larval and pupal stages rather than of variation in the egg laying periods of the previous year. Preliminary laboratory experiments (unpublished) with *Aedes aegypti* have indicated that the high density of larvae commonly observed in the Canadian Subarctic may be associated with variations in the rate of development within single pools.

The phenomenon of photoperiodism should be mentioned in relation to variations in development since it has already been described for *Aedes* mosquitoes (Baker 1935; Love and Whelchel 1955). Winter larvae of *A. triseriatus* Say that are inhibited in their development under natural conditions will pupate normally if the photoperiod is artificially extended. Love and Whelchel showed that photoperiodism did not affect the hatching of ova. The unexplainable inhibition of development of *A. hexodontus* in the early stages as compared with other associated species indicates the possible influence of photoperiodism on biological grounds. From a meteorological point of view however this is less likely. The daily rate of increase in the period of daylight decreases from approximately one per cent in April to less than 0.1 per cent throughout June at Fort Churchill. Since the development of *A. hexodontus* in the Subarctic is usually confined to the month of June, the immature stages would have to be sensitive to very small changes in photoperiod to cause any signficant variation in time of pupation under natural conditions.

Summary

1. Formulae for predicting mosquito emergence are suggested from three years' field observations on the development of *Aedes* species of mosquitoes at Fort Churchill, Manitoba.

2. The development of post-hatching stages of both males and females of *A. communis* could be described by a common mathematical curve provided that the immature stages were not subjected to temperatures above the optimum of the species.

3. Curves of development were drawn for the pest species at Churchill on the basis of emergences of each species in at least three pools having different thermal characteristics. Lower thresholds of development and products of time and temperature are tabulated for the periods of development of common species.

4. The tundra species of mosquito (*A. impiger* and *A. nigripes*) had lower thresholds of development approximating 34° F; the forest species (*A. communis, A. punctor, A. excrucians*) had a range of 38-40° F, except *A. hexodontus,* which appeared to have an exceptionally high value of 45° F.

5. The products of time and temperature for the period of development of both tundra and forest species where lower for the smaller than for the larger species. For the Fort Churchill area they were 260 to 440 degree-days for the common species of *Aedes*.

6. The peak emergence of *A. communis* males consistently preceded that of the females.

7. Mathematical descriptions were constructed for the relation between meteorological elements (temperature, dry cooling power of the atmosphere, and daily amount of sunshine) and the daily average of temperature of mosquito pools.

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THE FOOD OF SOME COLUBRID SNAKES FROM FORT BENNING, GEORGIA

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The food of colubrid snakes of the southeastern United States is not well known. While many accounts have appeared on snake dietary from this region, these usually are of a fragmentary nature, and generally have been incidental to taxonomic studies, annotated lists, or the like.

The Fort Benning Military Reservation is located in Chattahoochee and Muscogee counties, Georgia. The western boundary of the reservation touches the Georgia-Alabama State line. The principal area of study and collecting encompasses a 90 acre tract in Chattahoochee County (Long. 84′ 52″, lat. 32′ 25″), the so-called Magazine Area, just north of the old hospital grounds. The area is one of gently rolling hills with elevations of from 250 to 500 feet. Extensive stands of timber cover the greater part of the reservation. Prominent trees are the oaks, (white, water, post, red,