MICROCLIMATE AND ECOLOGY OF VECTOR BORNE DISEASE

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Appendix: Figures 1 to 34, which are placed in order following the text for ready reference.
ERRATA

Page 44, Line 9. *Aedes squamipennis*; should be *Aedeomyia squamipennis*.

Fig. 32: *Lutzomyia trapidoae*; should be *Lutzomyia trapidoi*.

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MICROCLIMATE AND ECOLOGY OF VECTOR BORNE DISEASE

Abstract

This was an interdisciplinary investigation of the relation of the microclimate and the ecology of insect borne disease in a rapidly changing tropical forest environment as a result of the construction of a hydroelectric dam and the creation of a man-made lake. About 300 Km$^2$ of tropical forest were inundated in the Bayano River Basin 70 Km east of the Pacific entrance to the Panama Canal. There were three main objectives. The first was to provide the background physical environmental factors for the study of ecological changes due to the formation of the man-made lake in the midst of the tropical forest. The years 1972 through 1975 were base line years of pre-impoundment. The years 1976 and 1977 were years of flooding, while 1978 was the first year of post-impoundment and stabilization. The microclimate of the forest in 1973 was one of relatively cool daytime temperatures and warm nighttime temperatures. There was very little wind and the air spaces within the forest were moist and stagnant. In 1974 and 1975 the daytime temperatures were warmer and the nighttime temperatures were cooler with increased daytime wind speeds at canopy level due to the severe cutting of forest in preparation for flooding. In 1976 and 1977 the temperature continued to rise and the spread between average maximum and minimum temperatures reached as high as 13 degrees. The winds also became much stronger and turbulent during the nighttime periods. In 1978 the forest continued to be warmer than in the early base line period before flooding. The
background physical environment which includes the moisture budget, radiation budget, vertical temperature structure, and the winds are presented in graphical form along with the text. The detailed day by day processed data format may be found in the reference library at Gorgas Memorial Laboratory, Panama.

The second objective was to prepare simple models for the use in the quantification of changes in the ecology of insect borne disease due to microclimate changes. The models indicate the man biting activity of phlebotomine and *Culicoides* vectors are dependent upon rainfall patterns, while mosquito biting activity is greater during the dry season.

The third objective was to examine the microclimate and the epidemiology of vector borne disease, and to offer a basis of predictability for similar engineering projects in tropical America. A model using the hygrothermal space coordinates of temperature and vapor pressure indicates the biting activity of the principal phlebotomine and mosquito species occurs in a very narrow range of temperature and vapor pressure. The model may be used in epidemiological surveillance work for insect borne zoonotic diseases. Once the matrix for a particular insect vector is established, then it may be possible to calculate the probability of being bitten by that vector and thus indicate one of the possible avenues in the transmission to man by measuring 2 simple physical parameters like vapor pressure and temperature.
1. Introduction:

The Republic of Panama commenced construction of a hydroelectric dam early in 1972 on the Bayano River about 70 Km east of the Pacific entrance to the Panama Canal. Subsequently, there was impoundment of 300 km$^2$ of tropical forest as a man-made lake was created up river from the dam site. As a result of this flooding, there were drastic ecological changes to the flora and fauna of the area. Two grants from the National Institute of Health (NIH) were awarded to the Gorgas Memorial Laboratory (GML) to investigate the Ecology of Vector-Borne Viruses in Panama: (AI-02984), Principal Investigator Pedro Galindo, and Microclimate and Ecology of Vector-Borne Disease (AI-11889), Principal Investigator, Robert G. Read. Both of these grants were made to investigate changes in the ecology and microclimate brought about by the construction of the dam. This report is concerned with the effects of the microclimate on the ecology of arthropod-borne diseases in the Bayano River Basin.

Three natural periods divided the investigation into a period of pre-impoundment 1972 through 1975, impoundment 1976 and 1977, and 1978 the first year of post-impoundment. The physical changes that occurred during these three periods were very apparent. In 1974 in the area near the field site there was a complete cutting of the forest up to the level at which the waters were expected to rise. The only uncut forest was on a high ridge overlooking the river where the Gorgas Memorial Field Station was located. This area was then known as Altos de Maje and consisted of untouched forest
overlooking the Kuna Indian Village of Maje at the junction of the
Bayano and Maje Rivers. Flooding began in February, 1976 and the man-
made lake continued to grow in size and finally reached stabilization
late in 1977.

At the historical junction of the Bayano and Maje Rivers
the island of Maje was formed and consisted of more than 5,000 acres
of untouched forest (Cuipo association). In 1976 as flooding pro-
gressed, the water surface in the lower Bayano Lake near the island
of Maje became covered with an aquatic fern of the Azolla sp. Early
in the period this fern like water plant covered the lake as if it
were a green rug and later in the year the color turned to red. In
1977 the lake was covered with large floating patches of water let-
tuce Pistia which moved from the north to the south sides of the lake
daily in response to water currents and the winds. By midsummer in
1978, the Pistia was under control and largely confined to the areas
where the Bayano and Maje Rivers entered the man-made lake.

In the planning stages, prior to the awarding of the
grant, it was expected that there would be drastic biological changes,
and much more subtle changes in the microclimate. It was expected
that as flooding progressed, the vertebrate fauna would move to higher
ground and that there would be a sharp increase in population den-
sities in the island study site. There would be an inter/intra spe-
cific struggle for vital living space which would continue until the
lake became stabilized and ecological equilibrium reached on the
island. This did occur and an animal rescue project, Project Noah II,
with private sponsorship undertook the rescue of animals displaced by the rising waters in 1976 and 1977. Many of the rescued vertebrates were released on the Maje Island field site.

With the flooding it was also expected that there would be an upsurge of flood plain mosquitoes seeking refuge in the forested hills of the island of Maje where there would be an abundance of vertebrates as a source of blood. As a result of the explosion of aquatic weeds (Pistia) there would be a sharp rise in the density of mosquitoes that breed in association with this aquatic weed. This was manifest in 1976 and 1977 when there was a tremendous population increase of Mansonia dyari.

It was expected that the physical environmental changes would be much less dramatic in appearance. There would be less marked seasonality in the climate; the winds would increase during the rainy season and the dry season temperatures would be cooler due to the presence of the man-made lake. The humidities were also expected to be higher. These changes were partially realized: The winds did increase noticeably during the rainy season, but there was little change in the humidity and the forest temperature structure actually became much warmer with greater diurnal ranges of temperature.

The Bayano River Basin was a huge natural laboratory in which insect-borne disease ecology could be examined. It is reasonable to assume that there is a necessary threshold level of a vector population that permits the subsequent passage of a pathogen
from host to host. The working hypothesis was that there was a
critical correlation between the microclimate in the forest and the
changing population densities of insect vectors of disease such as
mosquitoes, phlebotomines and Culicoides. These insects are so com-
pletely immersed in an atmospheric environment that accompanying
physical factors such as temperature, humidity, rainfall, evaporation,
radiation and winds play a decisive role in the population dynamics,
man biting activity, and, as a consequence, in the ecology of the
diseases carried by them.

There were three objectives: (1) To provide the back-
ground physical environmental factors for the study of ecological
changes and to determine the effect that the microclimate has on the
ecology of insect borne disease in a rapidly changing tropical forest
environment due to the construction of a hydroelectric dam and the
formation of a man-made lake. (2) To prepare mathematical models
of the microclimate for use in the quantification of any changes to
support the investigation of the ecology of vector borne disease.
(3) Investigate the influence of a changing microclimate on the
epidemiology of vector borne diseases and to offer a basis of pre-
dictability for similar engineering projects in tropical America.

Prior to this research effort no scientific investi-
gations had been carried out on the effects of the formation of a
large man-made lake on the ecology of transmission cycles of arbo-
viruses in the tropics. Most previous research had been oriented
to other biomedical aspects such as schistosomiasis, malaria, and
onchocerciasis (Lowe-McConnel, 1966), (Ackerman, White, and Worthington, 1973). The Bayano investigation was the first extended period study of microclimate within a tropical forest which permitted the close examination of the relationship between the physical environment and the arthropod-borne disease ecology. The arthropod hosts were viewed in their natural field environment where the physical factors of temperature, wind, rain, humidity, etc. were "controlled" by nature in a pre-flooding and post-flooding climate.

Adaptative changes in response to a changing physical environment is a major factor in the ecology of vector borne disease. Insects respond to temperature changes to the point where actual temperatures may be ascertained with considerable accuracy from certain insect activities (Mills, 1952). Longevity of sandflies under laboratory conditions correlate well with certain ranges of temperature and relative humidity, while in the forests of Panama, dryness or waterlogging of the forest floor due to scanty or excessive rainfall seems to reduce adult densities of sandflies (Chaniotis, 1967), (Chaniotis, B. et al. 1971). It is recognized that the combined effect of vertical gradients in light, temperature, and humidity have a major influence on insect vector activity (Reeves, 1965). There is a positive correlation between relative humidity and the distribution and abundance of Aedes vexans (Platt, R. B. et al. 1958). In the cloud forest of north central Venezuela (Scorza, J. V. et al. 1963) found that phlebotomine sandfly catches decreased appreciably with falling temperatures and relative humidities. In a
study of sandfly populations in a tropical forest of Panama (Rutledge and Mosser, 1972) show that the principal environmental factor affecting sandfly populations and species compositions in tree based habitats is that of protection from flooding during heavy rainfall. In an area of Panama through which sylvan yellow fever passed there are substantial year to year fluctuations in rainfall and correspondingly great fluctuations in the densities of arboreal mosquitoes known or suspected to be yellow fever vectors (Galindo, P. et al. 1956).

The rationale is an acknowledgment that the area affected by the construction of the hydroelectric dam would be so large and covered with such dense tropical forest prior to flooding that any complete ecological or microclimate investigation would be almost impossible. However, since the forest was relatively homogeneous, it was assumed that the effect of changes in the microclimate and corresponding ecological changes of insect-borne diseases would be adequately interpreted by sampling from a few stations. The field station at Maje was well located on a ridge near the river to give representative pre-impoundment climate measurements. When this site became an island, during and after impoundment, it was ideally suited to investigate the ecological successions that would take place in the fauna of the island and the fluctuations in the activity of insect-borne disease in the natural vectors and hosts as well as the changes brought about in the microclimate by flooding. The island post-impoundment climate would be representative of the
strip of land surrounding the lake and thus the area most exploit-
able by man. It would also provide a basis for a reasonable esti-
mate of the remainder of the flooded river basin. Resulting data
and analyses would be useful in predicting extended period changes
in the climate brought about by the creation of a man-made lake.
The variations in cyclical behavior of insect vectors would be influ-
enced largely by the winds, radiation and moisture budgets and the
vertical temperature gradient in the first 30 meters above the
forest floor.

2. Methods and Procedures:

In the fall of 1972, the principal microclimate station
was established on a hog-back ridge with forested slopes. From the
elevation and location, measurements would be representative of those
at the top of the forest canopy and, hence, of the free air flow in
the Bayano River basin. Daily measurements were made of the rainfall,
evaporation, wind and maximum and minimum temperatures. Measurement
of the temperature and relative humidity, solar radiation and rainfall
intensity was continuous. A secondary microclimate station was estab-
lished about 500 m in the forest from the main camp. There, a wooden
tower was erected extending 29 m into the canopy. At this tower 24-
hr insect collections were made every 2 wk by using man as live bait.
Hourly collections were made at the floor of the forest (1 m) and in
the canopy (23 m). The collections were placed in 2-dr screw-top
vials and frozen in liquid nitrogen for transportation to the central
laboratory for identification and virus isolation. Concurrently,
hourly observations were made of temperature and humidity at the same location.

The ambient air temperatures and humidities were matched with the number of each species collected at the two stations during the same time period. A matrix using temperature and vapor pressure as the independent variables, and the number of specimens collected of a particular species as the dependent variable, was used to develop a model of the thermal space. These temperatures and vapor pressures define the hygrothermal space in which the insects were collected during man-biting activity.

Daily measurements were made of forest rainfall, evaporation from the forest floor, and maximum and minimum temperatures at five different levels on the tower. From the comparison of measurements taken at those stations, the moisture and radiation budgets of the forest were computed. Wind measurements were taken daily, and hourly when necessary. A simple totalizing contact anemometer, which did not require the use of electric power, was used to measure wind speeds.

The anemometer was typical of the unsophisticated but practical instruments which were utilized, since the tropical forest environment is extremely hostile to complex instrumentation. At two-week intervals, all instruments were returned to the laboratory for cleaning, repair and calibration. For example, anemometers were changed to prevent errors in measurement, which might arise as bacteriological growth collected on the drive shafts. An anemometer left
in the field for a month would only measure about 50% of the daily air flow.

Other instruments, not routinely available, were fabricated and calibrated in the laboratory prior to being placed in the field. To accurately measure rainfall on the forest floor or the through fall of rain from the forest canopy, while it is raining, plus the dripping which reaches the ground during the period of measurement, it was necessary to design a collector with a surface sufficiently large to provide representative measurements. A rain gage was manufactured from heavy sheet metal, 10 m long and 10 cm wide, which was then located in a forest area representative of the canopy in general. Each liter of water collected indicated 1 mm of through fall.

It is difficult to measure evaporation under the best of conditions, but especially so in tropical regions with heavy rainfall. Black and white porcelain spherical evaporimeters were used to measure the potential evaporation. The spherical shape of these instruments approximated the natural evaporating surfaces and best suited the needs of practicability in measuring evaporation in a tropical forest (Read, 1968). The average amount of evaporation from the two evaporimeters was used to compute the mean net radiation. The black evaporimeter tended to maximize and the white evaporimeter to minimize the amount of radiation absorbed in the process of evaporation. The absorption of the natural evaporating surface of the forest was taken to be the average of the two instrument surfaces.
In the tropical forest the main method by which radiative surpluses of the vegetative surfaces are dissipated and transferred vertically to the atmosphere is by evaporation of water. Budyko (1956) and Sellers (1965) state that the potential evaporation from a fully wet surface is very closely related to the radiation budget of the wet surface. In fact, if all available radiative energy is used for evaporation and there are no other energy sources, the radiation budget is equal to the flux of latent heat. The assumption is made here that the radiation budget of the wet surface is a good approximation to that of the natural evapotranspiring surfaces in the tropical forest.

The radiation budget at the surface of the earth in a tropical forest may be written \( R = Q_s + Q_e + S \), where \( R \) is the net amount of radiation absorbed at the surface, \( Q_s \) the energy given off as sensible heat, \( Q_e \) the energy given off as latent heat, and \( S \) the storage of heat which may be neglected in the annual heat balance because heat stored in the morning and early afternoon is almost balanced by heat loss in the late afternoon and night (Sellers, 1965). On this basis the radiation budget becomes \( R = Q_s + Q_e \).

In the oceans equatorward of the subtropical ridge \( Q_s \) is about 0.1 \( Q_e \) (Simpson, 1970) and near the equator \( Q_s \) is about 0.05 \( Q_e \) (Sellers, 1965). In this tropical forest of Panama, which is at
about 9°N latitude, and never more than 50 mi from the ocean, a reasonable value for $Q_s$ is 0.1 $Q_e$.

Substituting LE for the flux of latent heat $Q_e$, where $L$ is the latent heat of vaporization and $E$ the potential evaporation, and using the ratio $Q_s/Q_e = 0.1$, the radiation budget becomes

$$R = 1.1 \text{ LE}.$$ 

Computations of the net radiation were made from the potential evaporation at the main climate station and on the floor of the forest at the tower location. It should be noted that the computations are order-of-magnitude solutions. Errors in measurement may occur during periods of heavy rainfall when, for example, on the forest floor no measurable evaporation takes place for several days and the air below the forest canopy is stagnant and humid.

Beginning in August, 1974 the incoming solar radiation ($R_0$) was measured at the main camp at a location that was representative of the top of the canopy. The net radiation (R) is a measure of the energy available at the surface of the earth for evaporation of water and the energy used in warming and expanding the air. The Albedo ($\alpha$) is a measure of the reflectivity of the forest and was computed using the evaporation measurements from the black and white evaporimeters. The back radiation ($R_B$) is a measure of how much of the incoming energy is re-radiated back to space. The net radiation budget (R) then can be written as:

$$R = R_0 (1 - \alpha) - R_B \left(\frac{\text{Watts}}{\text{m}^2}\right)$$
The term \( R_B \) is computed as a residual.

All of the meteorological data collected from 1972 through 1978 were processed and edited and placed on punched cards and tapes. Obvious observational and instrument errors were eliminated so that a complete and reliable data bank could be produced. Many of the observations had been taken using English units such as degrees Fahrenheit, and miles per hour. All such measurements were converted to Standard Index (SI) units. Smooth data formats were then prepared of daily and hourly measurements as well as average values with standard deviations. These data were all filed in indexed tabular form thus providing the detailed physical daily environment parameters for any period during the years 1973 through 1978 and may be found in the reference library, Gorgas Memorial Laboratory, Panama, Panama. Included are:

a) Radiation Budget of the Forest, 1 (m) and 29 (m) level.
b) Moisture Budget of the Forest, 1 (m) and 29 (m) level.
c) Temperature Structure of the Forest, 5 levels.
d) Winds.
e) Average 6 hr period weather elements during insect collections 1 (m) and 23 (m) level.
f) Diel Cycle of Insect that yielded virus and the weather elements.
g) Average arthropod collections/24 hrs.
h) Arthropod monthly average densities/6 hrs.

i) Arthropod monthly average densities/12 hrs with weather elements 1 (m) and 23 (m) levels.

3. Results:

The background physical environmental factors upon which the ecological investigations rest are shown in brief tables and in graphical form in the appendix, and are organized in the following order:


3. Average daily vertical temperature profile in the forest (5 levels) (1973 - 1978).

4. Average daily maximum and minimum temperatures at ground level and at top of the forest canopy (1973 - 1978).

5. Effective temperatures near the ground and in mid-canopy levels during 6 hour periods in 1977.


7. Average weather elements during collection periods near the ground and mid canopy levels for day (0600 - 1800) and night (1800 - 0600).

8. Average daily winds.

The monthly rainfall totals for the pre-impoundment period (1973 - 1975) are shown in Figure (1). The totals for the
Impoundment (1976 - 1977) and Post-impoundment (1978) periods are shown on Figure (2). The diagrams show the incoming rainfall at the top of the forest canopy as well as the rain which reaches the floor of the forest. The rainfall pattern is one in which there are usually four months of dry season from January through April and eight months of rainy season. December and April are transition months at the end and the beginning of the rainy season. The month of the heaviest rainfall is October. Using the monthly average rainfall amounts shown in Table (1) and a threshold value of 10 cm/month as an approximation of the beginning and end of the rainy season, it was determined that the beginning of the rainy season is April 20 \pm 10 days and the beginning of the dry season is December 14 \pm 10 days. These approximations were computed using the following monthly averages and the formulae

\[
\text{Day (Rain Season)} = \frac{D \left( T_0 - b \right)}{a - b},
\]

\[
\text{Day (Dry Season)} = \frac{D \left( a - T_0 \right)}{a - b},
\]

where \( T_0 \) = threshold value (10 cm/month), \( a \) = monthly average next above \( T_0 \), and \( b \) = next monthly average below \( T_0 \). \( D \) is the difference in days between the middle of the month with the average amount \( b \) or \( a \) and the middle of the subsequent month, i.e., \( D = 30 \) days.
Table (1)
Monthly Average Rainfall (cm) during the period
1973 - 1978 at Maje

<table>
<thead>
<tr>
<th>Month</th>
<th>Average (cm)</th>
<th>Month</th>
<th>Average (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>J</td>
<td>0.4</td>
<td>J</td>
<td>25</td>
</tr>
<tr>
<td>F</td>
<td>0.8</td>
<td>A</td>
<td>23</td>
</tr>
<tr>
<td>M</td>
<td>0.4</td>
<td>S</td>
<td>19</td>
</tr>
<tr>
<td>A</td>
<td>7.7</td>
<td>O</td>
<td>39</td>
</tr>
<tr>
<td>M</td>
<td>21.8</td>
<td>N</td>
<td>31</td>
</tr>
<tr>
<td>J</td>
<td>20.4</td>
<td>D</td>
<td>9</td>
</tr>
</tbody>
</table>

The yearly rainfall is shown in Table (2). Over the 6 year period about 62% of the rainfall reached the floor of the forest. A comparison of the two rainfall amounts shows how effective the forest is in the reduction of the amount of rainfall that reaches the ground in the forest. Not only the total amount of rain is reduced but the size of the large raindrops that fall during heavy showers is reduced to that of a spray and the velocity of the impact with the ground is also greatly reduced.

The moisture balance, which is defined as the difference between the amount of evaporation (E) and the amount of rain (R) over a given time, is of primary importance to the flora and fauna of the forest. When (E-R) is negative it signifies that there is an excess of rainfall, while a positive (E-R) is indicative of a
Table (2)
Annual rainfall at the top of the canopy and the ground in the forest

<table>
<thead>
<tr>
<th>Year</th>
<th>Top of Canopy</th>
<th>Forest Floor</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rain (mm)</td>
<td>% of Normal*</td>
</tr>
<tr>
<td>1973</td>
<td>1,918</td>
<td>102</td>
</tr>
<tr>
<td>1974</td>
<td>1,987</td>
<td>105</td>
</tr>
<tr>
<td>1975</td>
<td>2,613</td>
<td>138</td>
</tr>
<tr>
<td>1976</td>
<td>1,257</td>
<td>66</td>
</tr>
<tr>
<td>1977</td>
<td>1,647</td>
<td>87</td>
</tr>
<tr>
<td>1978</td>
<td>1,855</td>
<td>99</td>
</tr>
</tbody>
</table>

*1,880/1,177 mm is the average or normal rainfall for the 6 year period.

water deficit. The excesses and deficits cause a climatic stress that is realized by all living things in the forest. Figures (3, 4) show the moisture balance on a cumulative basis for a period of a year. There are two curves plotted for each year. One curve shows (E-R) at the top of the canopy while the other curve shows the moisture balance at the floor of the forest. The moisture balance on a time frame of one year may be quite useful. For example, when (E-R) is zero there is a balance between annual rainfall and evaporation. The figures at the end of the year show how much rainfall exceeded the evaporation for that particular year. In 1974 by the end of
January the evaporation (E) exceeded rainfall (R) by 110 mm. At the end of April this figure had increased to over 600 mm. At the end of June, as the rainy season brought more rain, the excess of evaporation was down to 200 mm. In the first week of August the rainfall for the year exactly balanced the evaporation for the year. At the end of October rain had exceeded evaporation by 700 mm, and at the end of December the yearly rainfall had exceeded the yearly evaporation by 835 mm. Table (3) summarizes the cumulative moisture balance.

Table (3)
Cumulative Moisture Budget 1973 - 1978

<table>
<thead>
<tr>
<th>Year</th>
<th>Forest Canopy</th>
<th>Forest Floor</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Month</td>
<td>End of Year</td>
</tr>
<tr>
<td></td>
<td>E = R</td>
<td>E - R</td>
</tr>
<tr>
<td>1973</td>
<td>June</td>
<td>(1,274)</td>
</tr>
<tr>
<td>1974</td>
<td>August</td>
<td>(835)</td>
</tr>
<tr>
<td>1975</td>
<td>August</td>
<td>(1,531)</td>
</tr>
<tr>
<td>1976</td>
<td>October</td>
<td>70</td>
</tr>
<tr>
<td>1977</td>
<td>October</td>
<td>(355)</td>
</tr>
<tr>
<td>1978</td>
<td>July</td>
<td>(735)</td>
</tr>
</tbody>
</table>

() Indicates (E-R)< 0

The rainfall in 1976 was only 66% of normal annual rainfall and this was the only year that the moisture budget was positive, i.e. evaporation exceeded rain. Nevertheless, in the forest near the ground, the moisture budget remained negative and the water needs of
the forest were still satisfied.

There is often the need to examine the moisture balance on the time frame of one month at a time. Figures (5, 6) show the moisture budget at two levels on a monthly basis. To illustrate, in 1975 for the month of April evaporation exceeded rainfall by 190 mm. The following month, May, rain exceeded evaporation by 70 mm. At the end of November rain exceeded evaporation by 660 mm. The shaded areas give an approximation graphically of how wet the rainy season was for a particular year. In using these last diagrams it should be realized that the data plotted are the cumulative (E-R) to the end of the month. Daily values may be examined in the meteorological Tables located in the reference library at Gorgas Memorial Laboratory.

The vertical profile of temperature in a forest during the daytime might be expected to be one in which the radiation temperatures of the forest canopy would be greater than the temperature at various levels below the canopy which are shaded from direct sunlight. This would give a daytime profile in which temperature increased with height, or an inverted temperature structure (inversion). At night the canopy temperatures would be lower due to greater radiative heat losses than at levels below the canopy. This is the normal pattern of the vertical temperature structure near the surface of the earth in vegetated areas.

With an inversion present in the forest the density structure is one in which warmer and lighter layers of air overlie
cooler and heavier air below. This leads to a stable atmosphere with little mixing or vertical motion taking place. When the temperature decreases with height this leads to a situation in which heavier and cooler air overlie layers of warmer and lighter air and may permit overturning and mixing of air depending upon the rate of change of temperature with height. In general, the pressure at any level in the atmosphere depends upon the weight of the columns of air above that level, so that pressure generally decreases with height. Instability arises when there is a marked difference in the rate of temperature change with height (lapse rate). For perfectly dry air with no heat loss or gain in the system, the temperature lapse rate is \(-1 ^\circ C/100\ m\). If the lapse rate is less than this, i.e., \(-0.5 ^\circ C/100\ m\) there is usually sinking motion and stagnant, stable conditions. If the lapse rate is greater, i.e., \(-1.5 ^\circ C/100\ m\), then there is usually upward vertical motions with turbulent mixing. The ambient free moving air outside of the restricted spaces of the forest is neither dry, nor can one truly say there is no heat loss or gain in the lower layers. In these tropical latitudes, the free air lapse rate is about \(-0.5 ^\circ C/100\ m\). This rather long explanation has been necessary to better understand the demonstrated vertical temperature profiles in the appendix.

In the forest at the tower station the maximum and minimum temperatures are observed at levels of 1 m, 6 m, 12 m, 16 m, 23 m and 29 m. The 23 m level is at about the middle of the canopy. The top of the canopy is 29 m. The measurement for this level was
taken at the main camp where the observation site was representative of the top of the canopy. The temperatures during the rainy season are shown in Figures (7, 8) and are based upon the averages at each level. Averages were computed at 10 day and 30 day intervals. During the 1973 rainy season the forest was cooler at all levels during the day than in any other year following. This was the period when very little of the natural ecology had been disturbed by man. The surrounding forest was uncut and the river was 2 Km distant. There was a pronounced inversion from 1 m to 6 m in the daytime and a very unstable layer from mid canopy 23 m to the top of the canopy 29 m. Thus the layer near the ground was very stable and stagnant while in the canopy there was potential mixing and turbulence. Temperatures at any level rarely exceeded 30 degrees. The range between nighttime minimum and daytime maximum was small. In general the lapse rate from the ground to 23 m was a temperature inversion both during the day and night period. The temperature increased by about 5 degrees from the ground to mid canopy level. This inhibited vertical mixing and evaporation and caused the air between these two levels to be stagnant and damp. These conditions are favorable for large populations of phlebotomine sandflies and Culicoides.

During 1974 when the only uncut forest in the area was in the 5,000 acres of the field site at Maje, the daytime temperatures at all levels increased and the range of temperatures from daytime maxima and nighttime minima increased. This pattern was also true in all succeeding years. A pronounced inversion was present
between the 16 m level and the free air above the canopy. In the lower levels the inversion was present but considerably less pronounced. Daytime temperatures were 30 degrees or greater while nighttime temperatures were 20 to 22 degrees. In 1975 the vertical temperature structure was similar to that of 1974.

During the early part of 1976 the flooding of the Bayano Basin began. The temperatures at all levels in the forest during the day were greater than during previous years. Along with temperatures higher than 30 degrees was a strong inversion between 16 m and 29 m so that in December the temperature differential was 8 degrees warmer. Nighttime minima remained the same as in previous years. The temperature structure in the following two years, 1977 and 1978, was similar to that of 1976.

During the whole period 1974 through 1978 the nighttime minima showed a near isothermal lapse rate with temperatures of 21 to 22 degrees. In 1973 the nighttime minima were higher than in the succeeding years.

The dry season temperature structure is shown in Figures (9, 10). The year of 1973 was the coolest, with a small range in day-night temperatures. The average yearly temperature structure of the forest is also shown in Figure 10. Changes are shown in the vertical profile of temperatures during the years 1973 - 1978. The nighttime lapse rates were very nearly isothermal. In 1973 the forest temperatures during the night at all levels were warmer than in any other year. With the man made changes of forest cutting and
flooding the daytime temperatures of the forest were appreciably warmer. At midcanopy level (23 m) the average yearly maximum temperatures were:

1973   30 degrees   1976   34 degrees
1974   32 degrees   1977   33 degrees
1975   33 degrees   1978   32 degrees

When the temperature structure of the forest is examined in this way, it is seen that changes have occurred during the period of study. Nighttime minima have decreased and daytime maxima have increased. The climate-induced stress may have influenced the ecology of the flora and fauna of this forested area.

The temperatures at ground level 1 m and at the top of the canopy 29 m are of particular interest. Figures (11, 12, 13, 14) show the average daily maximum and minimum temperatures by months during the period of investigation. The average daily temperature $(T_{\text{max}} + T_{\text{min}})/2$ are also shown. The plotted temperatures are the 30 day averages. The numbers plotted above and below the curves are the variations in 10 day averages and indicate how the averages varied during the month.

For purposes of illustration the temperatures near the forest floor will be used. As indicated previously, 1973 was cool during the day and warm during the night when compared to the following years. Table (4) shows temperatures for the month of April.

The average minimum temperature for the period 1974 through 1978 was about 22 $(\pm 2)$ degrees. The maximum temperature
Table (4)

Maximum - Minimum Temperatures - April - 1 m

<table>
<thead>
<tr>
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<tr>
<td>T max</td>
<td>28</td>
<td>32</td>
<td>34</td>
<td>34</td>
<td>34</td>
<td>31</td>
</tr>
<tr>
<td>T min</td>
<td>25</td>
<td>24</td>
<td>22</td>
<td>21</td>
<td>23</td>
<td>22</td>
</tr>
</tbody>
</table>

fluctuated appreciably throughout the year. During a 24 hour period there was as much as 13 degrees difference between the maximum and the minimum average temperature. The pattern is one in which the maximum temperature rises until the end of the dry season and then falls throughout the rainy season.

The difference in maximum temperatures between the top of the canopy and near the ground in the forest are shown for the month of July and October in Table (5).

Table (5)

Maximum Temperatures in July and October at the 29 m and 1 m levels

<table>
<thead>
<tr>
<th></th>
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<tbody>
<tr>
<td>July</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 m</td>
<td>27</td>
<td>30</td>
<td>35</td>
<td>36</td>
<td>37</td>
<td>37</td>
</tr>
<tr>
<td>1 m</td>
<td>25</td>
<td>28</td>
<td>30</td>
<td>33</td>
<td>31</td>
<td>28</td>
</tr>
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</table>

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</thead>
<tbody>
<tr>
<td>Oct.</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>29 m</td>
<td>27</td>
<td>36</td>
<td>33</td>
<td>35</td>
<td>36</td>
<td>37</td>
</tr>
<tr>
<td>1 m</td>
<td>25</td>
<td>29</td>
<td>28</td>
<td>30</td>
<td>31</td>
<td>28</td>
</tr>
</tbody>
</table>
During these months in the rainy season there is a pronounced daytime inversion of 2 to 7 degrees from the forest floor to above the canopy.

In an attempt to estimate the effective temperature as sensed by human beings in the tropical forest the actual air temperature, vapor pressures, and relative humidity were used to compute the effective temperature. The assumptions and computations are those of (Winterling, 1979). The sensation of increased heat with high humidity is related to the decrease in vapor pressure differential between skin moisture and the water vapor in the air. There is some critical value of the vapor pressure differential that divides the sensation of comfort from discomfort due to evaporational cooling. If the assumption is made that skin temperature is 35°C (95°F), then the saturated vapor pressure at that temperature is 56 mb. The moisture level that appears to separate effective evaporation of skin moisture (comfort) from reduced evaporation (discomfort) is the range of dew point temperatures 17-20°C (63-68°F). Using a dew point temperature of 18°C this gives a vapor pressure of 21 mb in the ambient atmosphere. The vapor pressure difference ($\Delta e$) between the skin at 35°C and the air at a dew point temperature of 18°C is 35 mb or (56 mb - 21 mb) = 35 mb. When ($\Delta e$) is less than 35 mb the air "feels warm and muggy", i.e., when $\Delta e >$35 mb evaporation is effective. Then the effective temperature is computed.

$$T_{eff} = T + (e - 21) \text{ degrees F}$$
The term \((e - 21) \text{ mb}\) is a measure of the effective evaporative cooling. One degree Fahrenheit is added to the air temperature for every millibar less than a \((\Delta e)\) of 35 mb. For this study the effective temperatures are computed in degrees Centigrade.

Figures (15, 16, 17, 18) show the effective temperatures near ground level and in mid-canopy level of the forest during 6 hour periods in 1977. The air temperatures at ground level between 2400 and 0600 are less than 26 degrees, but due to the high humidity the effective temperatures are about 29 degrees. From 0600 to 1200 the air temperatures are about 26 degrees while the effective temperature is about 31 degrees. During the dry season months, January through April, between 1200 and 1800 the air temperatures are 26 to 32 degrees, but the effective temperatures are 30 to 38 degrees. Throughout the year the effective temperature is about 33 degrees. During the evening period 1800 to 2400 the air temperature is about 26 degrees while the effective temperature is about 30 degrees. Thus throughout the year the daily effective temperatures range from 30 to 38 degrees \((86 - 100^\circ F)\). These temperatures are average temperatures during the month and individual hourly temperatures may be higher.

Ecological relationships are manifested not in a vacuum, but rather in a physico-chemical environment, which includes the factors of moisture, winds, solar and net radiation along with the biotic components which interact in a fundamentally energy dependent fashion. Thus, the radiation budget of the forest plays an
important role in the ecological system.

The average daily radiation budget by month for the period 1973 through 1978 is shown in Figures (19, 20). These curves represent the incoming energy ($R_o$), back radiation ($R_b$), Albedo or reflectivity ($\alpha$), and net radiation ($R$) at the top of the forest canopy. Since these values are all average values there is some small discrepancy in the computed monthly and yearly values of ($R_b$). Thus, in 1976 the average daily value of back radiation ($R_b$) is $200 \frac{\text{Watts}}{\text{m}^2}$ but the computation yields a value of $198 \frac{\text{Watts}}{\text{m}^2}$. The daily values listed in the Meteorological Tables in the reference library at Gorgas Memorial Laboratory are exact values on a day to day basis where ($R_b$) is computed as a residual. The following table summarizes the data shown in the figures.

<table>
<thead>
<tr>
<th>Year</th>
<th>Avg. Daily ($R_o$)</th>
<th>Avg. Daily ($R$)</th>
<th>Avg. Daily ($R_b$)</th>
<th>Avg. Daily ($\alpha$) (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1973</td>
<td>-</td>
<td>98</td>
<td>-</td>
<td>22</td>
</tr>
<tr>
<td>1974</td>
<td>-</td>
<td>104</td>
<td>-</td>
<td>21</td>
</tr>
<tr>
<td>1975</td>
<td>358</td>
<td>94</td>
<td>179</td>
<td>23</td>
</tr>
<tr>
<td>1976</td>
<td>404</td>
<td>117</td>
<td>200</td>
<td>22</td>
</tr>
<tr>
<td>1977</td>
<td>403</td>
<td>115</td>
<td>206</td>
<td>19</td>
</tr>
<tr>
<td>1978</td>
<td>382</td>
<td>99</td>
<td>202</td>
<td>22</td>
</tr>
</tbody>
</table>
Thus in 1977, of the 403 watts/m² average daily radiation the reflectivity of the forest was 19%, with about 77 watts/m² lost to space directly. The forest re-radiated back to space 206 watts/m² and 115 watts/m² were used by the forest as latent and sensible heat. (The error using yearly average is about 5 watts/m²).

Figures (21, 22) show the average daily net radiation, and Albedo at the floor of the forest with the incoming radiation at the canopy level. Numbers on the curves give the average daily values throughout the year. The following table summarizes these values.

Table (7)
Annual Average Daily Radiation Budget at the Floor of the Forest (Watts/m²)

<table>
<thead>
<tr>
<th>Year</th>
<th>Avg. Daily R (Forest Floor)</th>
<th>Avg. Daily R₀ (Canopy)</th>
<th>Ratio R/R₀ %</th>
</tr>
</thead>
<tbody>
<tr>
<td>1973</td>
<td>45</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1974</td>
<td>42</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1975</td>
<td>47</td>
<td>358</td>
<td>13</td>
</tr>
<tr>
<td>1976</td>
<td>48</td>
<td>404</td>
<td>12</td>
</tr>
<tr>
<td>1977</td>
<td>56</td>
<td>403</td>
<td>14</td>
</tr>
<tr>
<td>1978</td>
<td>39</td>
<td>382</td>
<td>10</td>
</tr>
</tbody>
</table>

In 1977 of the 403 watts/m² at the top of the canopy as incoming radiation only 56 watts/m² or 14% of the incoming
radiation was available to produce latent and sensible heat at ground level in the forest.

During the biweekly insect collections at the tower in the forest, the temperature and wet bulb temperature were recorded every hour at the 1 m and 23 m levels. From these measurements the relative humidity, dew point, and vapor pressure were computed. Figures (23, 24, 25, 26, 27, 28, 29, 30) show the average weather elements during selected years between the hours 0600-1800 and 1800-1600. The weather elements at the 1 m level will be examined here. To establish a daytime reference value the base line temperature was 27 degrees, relative humidity 85%, and vapor pressure of 30 mb. The years 1973 and 1975 are the beginning and end of the pre-impoundment period, 1976 is the first year of impoundment and 1978 is the year of stabilization. The relative humidity is used to give the degree of saturation of the air, and the vapor pressure is used as the measure of the actual amount of water vapor in the air.

The daytime temperatures are higher than 27 degrees during the dry season and lower in the rainy season. Daytime relative humidities are usually less than 85% and values of 70 to 80% are quite common. During the rainy season in 1973 and 1976 values greater than 90% were seldom observed while in 1975 and 1978 values greater than 90% were common. In 1973 and 1978 the vapor pressure average throughout the year remained near the base line value of 30 mb. In 1975 and 1976 the vapor pressures were generally several millibars higher or lower than 30 mb. For example, in February and
April 1975 the vapor pressure was about 25 mb and in June 1975 it was 33 mb.

During the nighttime hours (1800 - 0600) lower base line values of temperature (25 degrees), vapor pressure (28 mb) were used while base line relative humidity was raised to 90%. The nighttime temperatures in 1973 were warm and averaged 25 degrees. In 1975 and 1976 the average temperature was one degree cooler or 24 degrees. In 1978 it was about 24.5 degrees. The relative humidities seldom reached 99-100%. Values less than 90% were common during the dry season and in the rainy season values of 90 to 97% were common. Vapor pressures in 1973 and 1978 were higher than 28 mb and lower in 1975. In 1976 the dry season values were less than 28 mb and in the rainy season they were higher.

The winds were measured at the main camp. They were representative of the free air flow above the canopy. There are no winds as such in the forest near the ground, but when the winds are relatively strong above the forest there is some ventilation which does penetrate to the floor of the forest. In general, it can be said that the air in the forest is stagnant and there is no organized air flow, i.e. speed or direction that can be measured. The average daily wind speeds are shown in Figure (31). Wind directions are from the north + 45 degrees except shortly before heavy rain showers when the winds shift to the southwest. The average wind speeds are shown in units of Km/day with the high and low daily wind speed for the month. To illustrate the use of this graph the wind speeds in April
1977 are used. The average daily wind speed is 156 Km/day (6.5 Km/hr). During the month there was one day with 291 Km/day (12 Km/hr) and another with 54 Km/day (2 Km/hr).

During the rainy season May through December the wind speeds are low. In 1973 when the forest was more or less untouched in the vicinity of Maje the wind speeds rarely averaged 25 Km/day (1 Km/hr). In 1974 and 1975, after surrounding forest had been cut, the winds increased to greater than 25 Km/day during the two rainy seasons. After flooding in 1976, the rainy season winds remained about the same as in 1975. The wind speeds recorded in the latter half of 1977 rainy season were unreliable due to malfunction of equipment.

The winds during the dry season are much stronger as a larger amount of the energy from the sun goes into the production of sensible heat which causes expansion of the air and gusty turbulent winds. The greatest wind speeds usually occur in March and April. Low wind speeds during the dry season are usually associated with cloudy days or rainfall. Once the ground is wet much of the energy from the sun is used in the production of latent heat as the water evaporates. Dry season winds of 1977 were much greater than the winds for any other year.

4. Discussion:

An excess of the water needs of the forest exists in Maje and this becomes apparent when the moisture budget (Evaporation-Rain) is examined. Every year except 1976 ended with a surplus of
rainfall. Some of this water surplus is accounted for in the runoff of the ground water while part of it is stored in the soil and in the trees themselves. Rainfall deficits are present during the first half of the calendar year and may exist until July or August or even until October when the yearly cumulative rainfall equals the cumulative evaporation for the year. There does not appear to be any significant change in the annual rainfall patterns during the six year periods that can be attributed to local conditions such as cutting of the forest or the creation of a man-made lake of about 300 km$^2$; however, the cutting of the forest in 1974 and the flooding during 1976, 1977 and 1978 produced quite noticeable changes in the temperature structure of the forest. Maximum temperatures were higher and minimum temperatures lower.

While the forest stores very little heat over a 24 hour period, the water in the lake stores large amounts of daytime heat in the upper surface layers and acts as a heat exchanger to the atmosphere at night. The nighttime temperatures might be expected to be warmer in the nearby forest while actually they were cooler than during the 1973 period when the area was little changed by man. The heat losses of the lake at night were utilized in two ways. The sensible heat added to the atmosphere caused a nighttime thermal wind circulation as the air expanded and the winds were much greater after flooding began. In addition to the increasing winds, the air over the lake was warmed enough at night so that cooling to the point of condensation did not occur.
There was normally no wind flow during periods of darkness during the rainy season in the pre-impoundment years 1973 through 1975. During this period heavy fog or low clouds formed at night in the lower elevations of the river valley. Below the main camp at Maje there was a heavy fog which completely obscured the valley. Fog usually started to form between 2200 and midnight as the downslope drainage of air settled to the valley and persisted until about 0830. After sunrise, at about 0600, the air temperature remained cool and no measurable wind was observed until the fog had almost evaporated. At that time, the anemometer began to turn slowly and air temperatures started to rise. During the years 1976, 1977 and 1978, there were very few occurrence of fog over the lake surrounding Maje Island.

After flooding the wind flow was measured at 0700 and 1800 daily as a cooperative measurement for the Panamanian Government. During the impoundment and post-impoundment periods the winds at night were much stronger and turbulent. Table (8) illustrates the day and night winds for selected days in 1979. For example, on March 27 of the 163 Km of wind flow post the station, 112 Km passed during the day and 51 Km during the night. During the rainy season on August 20 the wind flow during the day period was 21 Km and at night 6 Km.

The function of a forest in the radiation balance is to provide shade, and it is the tree canopy which causes an entirely different climate within the forest. This climate is energy dependent
Table (8)

Winds measured as total wind flow in Km/day (0700 - 1800) and night (1800 - 0700)
1979

<table>
<thead>
<tr>
<th>Date</th>
<th>0700 - 1800</th>
<th>1800 - 0700</th>
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<tbody>
<tr>
<td>March 25</td>
<td>32 Km</td>
<td>12 Km</td>
</tr>
<tr>
<td>26</td>
<td>74 Km</td>
<td>38 Km</td>
</tr>
<tr>
<td>27</td>
<td>112 Km</td>
<td>51 Km</td>
</tr>
<tr>
<td>28</td>
<td>219 Km</td>
<td>160 Km</td>
</tr>
<tr>
<td>April 9</td>
<td>116 Km</td>
<td>104 Km</td>
</tr>
<tr>
<td>10</td>
<td>137 Km</td>
<td>52 Km</td>
</tr>
<tr>
<td>11</td>
<td>90 Km</td>
<td>101 Km</td>
</tr>
<tr>
<td>12</td>
<td>178 Km</td>
<td>24 Km</td>
</tr>
<tr>
<td>August 19</td>
<td>22 Km</td>
<td>13 Km</td>
</tr>
<tr>
<td>20</td>
<td>21 Km</td>
<td>6 Km</td>
</tr>
<tr>
<td>21</td>
<td>8 Km</td>
<td>3 Km</td>
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<td>22</td>
<td>21 Km</td>
<td>1 Km</td>
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and the air temperatures and humidities depend upon how much energy is available below the forest canopy as sensible and latent heat. The average daily net radiation (R) at the top of the canopy was 133 watts/m² while in the forest near the ground it was 46 watts/m². It is only necessary to go from the bright sunlight near the edge of the forest to a few hundred meters within the forest to sense this
difference using the human body as a sensor. Air temperature may be
10 degrees cooler and so long as there is no physical activity the
feeling is one of relative comfort. The moisture content of the air
near the ground is such that the effective temperature never falls
below 30 degrees. When engaged in physical work within the forest
the sensation is similar to that when exercising in a steam bath.
Once the body is completely covered with sweat, evaporative cooling
is very small and the effective temperature loses its significance
as a measure of environmental conditions.

Insects as vectors of arboviruses may be limited in
space and in numbers by many factors which are not directly asso-
ciated with the microclimate. In general, however, they are so com-
pletely imbedded in the atmosphere that the atmospheric factors must
be considered of great importance in controlling the occurrence and
abundance of the insects, and to some extent the distribution and
mobility of the arboviruses. Flying, crawling, and biting activity
of mosquito and phlebotomine populations are related to a physiologi-
cal cycling that depends largely on starvation, age, and consumation
of activity pertaining to the period preceding the time of measure-
ment. The cycle of behavior may be modified, and completely or in-
completely inhibited by weather conditions to varying degrees for
short intervals of time (Haufe, 1967).

In the tropical forest where the atmospheric variables
of temperature and humidity are warm and wet most of the year the
conditions are favorable for large populations of mosquitoes and
phlebotomine species at different times of the year. A model of a
hygrothermal space was developed using temperature and vapor pressure
as independent variables. The number of specimens of a particular
species collected using man as live bait was used as the dependent
variable. The working hypotheses were: 1. The variation in adult
insect man-biting activity is greatly dependent on environmental
temperature and humidity; and 2. Each species will "occupy" a
certain region in the hygrothermal space of temperature and vapor
pressure, all other conditions being equal, when engaged in such
activity, and may migrate in a vertical direction to find the region,
if a suitable host is available.

The approach was to quantify the physical atmospheric
variables so they could be used to explain ecological changes affect-
ing the man-biting activity of mosquitoes, phlebotomines, and
Culicoides sandflies in the tropical forest. The model is described
in detail (Read, R. G. et al. 1978).

Figures (32) and (33) show the ranges of air tempera-
tures and vapor pressures for several species of mosquitoes, phle-
botomines and Culicoides, at two levels in the forest during man-
biting activity. The total percent of the collection engaged in such
activity within those ranges is shown in the last column. The model
indicates that the range in which biting activity occurs is narrow.
In the canopy in 1973, 89% of the Haemagogus equinus were collected
when the temperature was greater than 24.8 degrees and 87% when the
vapor pressure was greater than 28.4 millibars. On the other hand, at
the same time and location, 97% of the Culicoides diabolicus were collected when the temperature was less than 26.4 degrees and 84% when the vapor pressure was less than 28.4 millibars. The data collected and the methods used were designed to represent the man-biting activity of several insect populations. Models of this type permit easily understood analysis of vast amounts of data that may have been accumulated. They may permit prediction of future patterns of these species where only small samples can be collected over a short period of time.

The model may be used in epidemiological surveillance work for insect-borne zoonotic diseases. Once the matrix for a particular insect vector is established, it may be possible to calculate the probability of being bitten by that vector and thus indicate one of the possible avenues in the transmission to man.

Some insect vectors are either daytime or nighttime biters. Time of day in addition to indicating periods of light or darkness may also imply warm temperatures and low relative humidities in the daytime and the opposite at night. Temperature, humidity, rain, and the other atmospheric parameters are real and physical variables that can be measured by man and sensed by the insects. The biting preferences of certain selected species during the period October 1972 to January 1978 are shown in Table (9) along with the temperature and the temperature of the dew point measured when the biting activity was at a maximum. The ranges of temperatures and dew point temperatures at which some man biting activity occurred is also
Live bait.

Range of temperatures and dew point temperatures when the insect was collected using man as a

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</thead>
<tbody>
<tr>
<td>16-28</td>
<td>97</td>
<td>22-24</td>
<td>24-26</td>
<td>33</td>
<td>20-33</td>
<td>20-30</td>
</tr>
<tr>
<td>16-26</td>
<td>59</td>
<td>20-22</td>
<td>22-24</td>
<td>49</td>
<td>24-26</td>
<td>20-30</td>
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<td>18-30</td>
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<td>22-22</td>
<td>170.573</td>
<td>42</td>
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</table>

Table (9)

Temperature and dew point temperature when biting activity was at a maximum

Species

<table>
<thead>
<tr>
<th>Hemagogus Yuketer</th>
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</thead>
<tbody>
<tr>
<td>Mansonia Dyer</td>
</tr>
<tr>
<td>Lutzomyia Pessona</td>
</tr>
<tr>
<td>Lutzomyia Panamensis</td>
</tr>
<tr>
<td>Lutzomyia Trapidoi</td>
</tr>
<tr>
<td>Lutzomyia Sanchez</td>
</tr>
<tr>
<td>Cuticoides diaper</td>
</tr>
</tbody>
</table>

[^1]:
shown. The data are normalized (% of the total collected) so that the various species can be compared. The temperature of the dew point is a measure of the water vapor present in the air as a gas. When the temperature of the dew point is equal to air temperature, condensation may occur. Higher dew point temperatures may be expected during the daytime hours as moisture is evaporated into the air, while lower dew point temperatures may be expected at night when condensation occurs on the natural surfaces in the forest. Dew point temperatures are more conservative than are the air temperatures which respond more readily to changes in the intensity of sunlight or other energy sources. Certain ranges of dew point temperatures appear to correlate well with maximum biting activities of the various insects. In the detailed analyses which are on file in the reference library at Gorgas Memorial Laboratory it is shown that Culicoides diabolicus, Lutzomyia pessoana, Lutzomyia trapidoi, Lutzomyia sanguinaria, Mansonia dyari, and Lutzomyia panamensis are nighttime biting insects. Haemagogus lucifer is a daytime biter.

Most of the nighttime biters show peaks of maximum biting activity when the dew point temperature is in the range of 20 to 22 degrees. *L. panamensis* shows peak of activity when the dew point temperatures are 22 to 24 degrees; however, 96% of the *L. panamensis* were collected when the dew point temperature was in the range of 18 to 24 degrees indicating the insect is a nighttime biter. *H. lucifer* is a daytime biter and also shows maximum biting activity in the dew point temperature range 22 to 24 degrees, but 74% of the
H. lucifer were collected when the dew point temperature was in the range of 22 to 28 degrees indicating that this insect is a daytime biter.

Most of the nighttime biters show peaks of maximum biting activity when the temperature is in the range 22 to 24 degrees. L. panamensis and M. dyari show peaks of maximum biting activity when the temperature is in the range of 24 to 26 degrees; however, 87% of the L. panamensis and 91% of the M. dyari were collected when the temperature range was 20 to 26 degrees indicating that these insects are nighttime biters. H. lucifer also shows maximum biting activity in the temperature range 24 to 26 degrees, but 85% were collected when the temperature range was 24 to 32 degrees indicating that this insect is a daytime biter. The data suggests that these temperatures and dew point temperatures may be the atmospheric stimuli for maximum biting activity.

Some insect vectors engage in man-biting activity when the rainfall is high while others do not seem to be affected by rainfall amounts. For example, 99% of the C. diabolicus collected during the years 1973 - 1977 occurred when it rained on the day of the collection or on the day before the collection.

The cumulative totals of all the mosquitoes and phlebotomine species are shown in Table (10).

If the assumption is made that one will be bitten by at least one mosquito and one phlebotomus during the year, then in the period of January through June, when about 25% of the yearly rainfall
Table (10)

Cumulative totals of man-biting collections 1972 - 1977

<table>
<thead>
<tr>
<th>Month</th>
<th>Mosquitoes Cum. %</th>
<th>Phlebotomines Cum. %</th>
<th>Rainfall Cum. %</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>12</td>
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<tr>
<td>2</td>
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<tr>
<td>4</td>
<td>70</td>
<td>1</td>
<td>3</td>
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<tr>
<td>5</td>
<td>79</td>
<td>2</td>
<td>14</td>
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<td>6</td>
<td>83</td>
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<td>84</td>
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<tr>
<td>11</td>
<td>96</td>
<td>97</td>
<td>96</td>
</tr>
<tr>
<td>12</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

has occurred, there is a very low probability (16%) of being bitten by a phlebotomus and a high probability (83%) of being bitten by a mosquito. A contingency table to show the probability (%) of being bitten in any one month of the year and the % of total annual rainfall for that month is shown in Table (11).

The table shows that the probability of being bitten in August, when about 12% of the annual rainfall occurs, is 20% for a phlebotomine, 18% for a Culicoides, and only 4% for a mosquito.
Table (11)

<table>
<thead>
<tr>
<th>Month</th>
<th>Phlebotomine % Year</th>
<th>Culicoides % Year</th>
<th>Mosquitoes % Year</th>
<th>Rain % Year</th>
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<td>20.17</td>
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<td>3.39</td>
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</table>

This type of modeling is useful for epidemiological surveillance work for insect borne diseases. There are problems when all species of mosquitoes and phlebotomus are considered together, since one species may be dominant. In this study of more than 500,000 mosquitoes collected using man as live bait more than 245,000 Mansonia dyari were collected in 1976 and 1977 at the canopy level.
The tables, however, demonstrate the high correlation of phlebotomine biting activity and monthly rainfall amounts and shows how the mosquito biting activity is greater during months with little rainfall.

During the year 1977 the collections of *Mansonia dyari* using man as live bait were very high. The presence of *Pistia* on the lake near the island produced ideal conditions for population explosions of this mosquito. Since the data showed that this mosquito bites more frequently in the dryer months of the year, it was of interest to determine how the evaporation rates were correlated with the biweekly collections of *Mansonia dyari*. The following linear relation was determined using the rate of evaporation over the period of the day before and the day of the collection:

\[ Y = -536 + 1037 \times X \]

Where \( Y \) = number of *Mansonia dyari*/24 hrs and \( X \) = the evaporation (mm)/48 hrs. The minimum value limiting the use of this equation is 0.5 mm/48 hrs of evaporation. That is to say that there must be at least 1/2 of a millimeter of evaporation during the 48 hours which always occurs in this locality. To test the goodness of fit of this linear regression line the correlation coefficient was computed as \( r = 0.81 \). This means that 66% of the variation in the collections is accounted for by the evaporation rate. This is an example of the correlation with the other factor in the moisture budget. The method is a measure of the biting activity of this mosquito, and it gives a relative estimate of the population size. The
basic assumption is that the other environmental factors are favorable for large population densities. An example of the use of this equation may help to explain its use. In June 1977 in the rainy season during one collection day the evaporation rate was 3 mm/48 hrs and the size of the collection was 1,235 mosquitoes. Using the equation the best estimate for the number collected would be 2,573 mosquitoes. In March 1977 during one collection period there were 18 mm/48 hrs of evaporation and 19,129 mosquitoes collected. The equation gives an estimate of 18,130 mosquitoes collected. It has potential epidemiological applications in that it indicates the times of the year to expect large populations and biting activity, and aids in the analysis of the structure of potential disease ecosystems. Furthermore, if there are negative results from the use of this equation, other biological or environmental factors are indicated as being more important at that time.

5. Conclusions:

When a project to build a large hydroelectric dam in the tropics is announced, it is only a matter of time before warnings are forthcoming on the possible consequences thereof. Often these are concerned with insect carriers of disease. Studies bearing on the ecology of an area to be flooded should be initiated at an early stage of dam development, so that forecasts based on data analyses can be taken into account to minimize health hazards and to prepare models for use in other projects. Such biological studies must be concerned with the physical factors of the microclimate and
its changes, since these atmospheric variables are likely to control, to a large extent, the density fluctuations in the populations of insect disease carriers.

The changes in the ecological system with impoundment were drastic and readily identifiable. Prior to 1975 there were essentially no *Mansonia dyari* mosquitoes, but in the years 1976 through 1978 the average density in the canopy during the night (1800 - 0600) was 1380/12 hrs. During the same period the average density of *Aedes squamipennis* was 105/12 hrs where it had been zero prior to those years. In 1973 the average density of *Culicoides diabolicus* in the canopy during the night was 9,314/12 hrs. In 1974 after the surrounding forest had been cut the average density was 2,051/12 hrs. With flooding in 1976, the average density was 52/12 hrs. Several other dramatic changes in the insect populations could be described. The changes in the microclimate were much more subtle, but some important elements changed noticeably. The nighttime fog disappeared almost completely with the appearance of the man-made lake within the watershed. At the same time the nocturnal winds, which had previously been absent, became quite strong and turbulent. Another unexpected change was the daytime warming and the pronounced temperature inversions in the forest. These changes were induced by man and may be expected to occur with any future construction of hydroelectric dams in tropical forested areas when the size of the impoundment is appreciable.
Acknowledgment

I would like to express my appreciation to Pedro Galindo for invaluable assistance in the field and in the laboratory as the Principal Investigator of his Grant AI-02984, Ecology of Vector Borne Viruses in Panama.
REFERENCES:


FIG. 2
ANNUAL RAINFALL 1976 - 1978

FOREST FLOOR RAINFALL
1976: 884 mm
1977: 1234 mm
1978: 1067 mm

FOREST CANOPY RAINFALL
1976: 1257 mm

IMPOUNDMENT - PERIOD 1976 - 1977
1647 mm

POST-IMPOUNDMENT
PERIOD 1978
1855 mm
FIG. 6

FOREST CANOPY (20m)

MOISTURE BUDGET (EVAPORATION - RAIN)

FRMAMJJASON DJFMAJASON DJFMAJASON
FIG. 9
TEMPERATURE STRUCTURE IN THE FOREST

<table>
<thead>
<tr>
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<th>Jan</th>
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</tbody>
</table>

Temp°C

Tmax
Day
Tmin
Night

Temp°C
Yearly Averages: Temperature Structure in the Forest

Temperature Structure in the Forest (Dry Season)
FIG. 15
EFFECTIVE TEMPERATURES, 2400-0600
MID-CANOPY LEVEL (23 m)
GROUND LEVEL (1 m)

1977

TEMP °C

38 36 34 32 30 28 26 24 22
J F M A M J J A S O N D

--- EFFECTIVE TEMP °C
- - AIR TEMP °C
Fig. 16

Effective Temperatures, 0600-1200

Air Temp. °C
Effective Temp. °C

Ground Level (1m)

Mid-Canopy Level (2.3m)

1977

(0600-1200)
Fig. 18

Effective Temperatures, 1800-2400

mid-canopy level (23 m)

ground level (1 m)

Air Temp. °C

Effective Temp. °C

1977

(1800 - 2400)
FOREST CANOPY (2m)
AVERAGE DAILY RADIATION BUDGET
FIG. 20
FIG. 27
AVERAGE WEATHER ELEMENTS (18-06) ON COLLECTION DAYS
1973

TEMPERATURE °C

RELATIVE HUMIDITY %
CANOPY LEVEL (23 M)

VAPOR PRESSURE (mb)

GROUND LEVEL (1M)
Fig. 28
Average Weather Elements (18-06) on Collection Days
1975

- Temperature °C
- Relative Humidity %
- Vapor Pressure (mbar)

Graphs showing
ground level
(1 m)
and canopy level
(23 m)
over time.
Air temperatures observed during insect collections at two levels in the forest showing the percentage of the total of each species collected in the range of temperatures indicated.

**LOCATION**

**Forest Canopy**
- Culicoides diabolicus: 1973, 23.0, 23.1, 24.8, 26.4
- Culicoides pifanoi: 1973, 1974
- Lutzomyia sanguinaria: 1973, 1974
- Lutzomyia trapidoae: 1973, 1974
- Lutzomyia ovallesi: 1973, 1974
- Haemagogus equinus: 1973, 1974
- Haemagogus lucifer: 1973, 1974

**Location Forest Floor**
- Culicoides diabolicus: 1973, 1974
- Lutzomyia panamensis: 1973, 1974
- Haemagogus equinus: 1973, 1974
- Haemagogus lucifer: 1973, 1974

Temperature (°C)

- 21.4
- 23.1
- 24.8
- 26.4
- 28.5
- 29.8
- ≥ 29.9

We collected:
- 97
- 99
- 95
- 97
- 93
- 97
- 95
- 99
- 97
- 97
- 89
- 90
- 90
- 86
- 91
- 92
- 94
- 97
- 88
- 96
- 88
- 87
FIG. 33  Vapor pressures observed during insect collections at two levels in the forest and the percentage of the total of each species collected in the range of vapor pressures indicated.

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FIG. 34  Manson 

M. dyari/24 hr Collections and evaporation on the day before and day of collection (Evap/48 hr)

\[ y = -522 + 1035 x \]

Evap. (MM/48H.)