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A Model of Microenvironment and Man-Biting Tropical Insects[1, 2]

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ABSTRACT

A hygrothermal space is developed in a model to show that adult insect man-biting activity is largely dependent on the environmental conditions of temperature and vapor pressure. Data collected in the tropical forest of the Bayano River Basin, Republic of Panama in 1973 are used to develop the model. Data acquired in 1974 are used to test the model. The data show that the most abundant insect species collected prefer narrow ranges of temperature and vapor pressure when engaged in man-biting activity. Certain *Culicoides* and phlebotomine species occupy the cooler and drier region of this hygrothermal space, while mosquitoes occupy a warmer and more humid region. Separation into definite regions is clearly shown with some overlapping in the middle range of temperature and vapor pressure.

The model presented 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.

The construction of a large hydroelectric dam and the formation of a 300 km² man-made lake in a tropical forest of the Bayano River Basin, 70 km east of the Pacific entrance of the Panama Canal, has dramatically changed the density of insect populations normally found in the area. Subtle and less noticeable changes in the microclimate may be a major factor controlling the population dynamics of insect disease vectors in the area. There are many studies which indicate the importance of the physical environment as an important factor in the abundance and diversity of insect populations (Smith 1954, Mills 1952, Dirmhirn 1961, Janzen and Schoerer 1968, Platt et al. 1958, and others). An excellent review article on the ecology of mosquitoes (Reeves 1965) indicates the importance of vertical gradients of light, temperature, and humidity on mosquito vector activities.

All animals are coupled to their physical environment by the flow of heat, gases, and nutrients. There is no animal so perfectly insulated that it does not exchange heat with its surroundings, and thus its internal temperature is affected by such factors as air temperature, humidity, and wind speed. It is thus important to quantify those paths of heat flow between animal and environment in order to define the relative importance of internal and external factors in the animal's ability to adapt to various microclimates (Spotila et al. 1972). Models should be developed to quantify how insects adapt to their environment.

The hypotheses to be tested here are: 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 that region, if a suitable host is available.

The approach is to *quantify* the physical atmospheric variables into models which can be used to explain ecological changes which affect the man-biting activity of mosquitoes, phlebotomines, and *Culicoides* sandflies in the tropical forest.

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Methods

In 1972 the Gorgas Memorial Laboratory Bayano project field station was constructed on a ridge of ca. 140 m elevation overlooking the Bayano River. During 1972 and 1973, a microclimate station was established at the main camp to measure the free air flow, humidity, temperature, evaporation, and rainfall above the surrounding canopy of the forest.

Forest towers and instrument platforms were manufactured and erected during this period. One forest tower was built ca. 30 m above the ground to make insect collections and to measure the microclimate through the vertical ascent from the forest floor to the canopy.

At this tower 24-h insect collections were made every 2 wk by using man as live bait. Hourly collections were made at the floor of the forest (one m) and in the canopy (30 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 at the same locations, hourly observations were made of temperature and humidity.

The ambient air temperatures and humidities were matched with the number of each species collected at these stations during the same time period, A matrix using 1973 data of 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 the model. Similar matrices using 1974 data were used to test the model for stability. The ambient air temperatures and vapor pressures used as coordinate axes in the model were those actually experienced in the forest locations throughout the year. These temperatures and vapor pressures define the hygrothermal space in which the insects were collected during man-biting activity in 1973 and 1974.

Results

Tables 1, 2, 3, and 4 are examples of the 1974 matrices for collections of *Culicoides diabolicus* and *Haemagogus lucifer*. Tables 1 and 2 show the hygrothermal space occupied by *C. diabolicus* at the forest floor and canopy stations. Tables 3 and 4 show the hygrothermal space occupied by *Haemagogus lucifer*. The matrices indicate that *C. diaboli-*

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Table 1.—Vapor pressure-temperature space, forest floor station, 1974, *Culicoides diabolicus*.

Vapor pressure (millibars)	Temperature °C < 18.0	18.0 19.6	19.7 21.3	21.4 23.0	23.1 24.7	24.8 26.4	26.5 28.1	28.2 29.8	> 29.9	Missing	Total
< 22.4	—	—	175.	—	—	—	—	—	—	—	175.
22.4–23.3	—	—	—	—	—	—	—	—	—	—	—
23.4–24.3	—	—	99.	201.	—	—	—	—	—	—	300.
24.4–25.3	—	—	—	67.	—	—	—	—	—	—	67.
25.4–26.3	—	—	—	—	312.	—	—	—	—	—	312.
26.4–27.3	—	—	—	197.	336.	128.	—	—	—	—	661.
27.4–28.3	—	—	—	—	1866.	22.	—	—	—	—	1888.
28.4–29.3	—	—	—	—	—	72.	—	—	—	—	72.
29.4–30.3	—	—	—	—	46.	4.	—	—	—	—	50.
30.4–31.3	—	—	—	—	—	—	4.	—	—	—	4.
31.4–32.3	—	—	—	—	—	—	—	—	—	—	—
32.4–33.3	—	—	—	—	—	—	3.	—	—	—	3.
33.4–34.3	—	—	—	—	—	—	—	—	—	—	
34.4–35.3	—	—	—	—	—	—	—	—	—	—	
35.4–36.3	—	—	—	—	—	—	—	—	—	—	
36.4–37.3	—	—	—	—	—	—	—	—	—	—	
37.4–38.3	—	—	—	—	—	—	—	—	—	—	
38.4–39.3	—	—	—	—	—	—	—	—	—	—	
> 39.4	—	—	—	—	—	—	—	—	—	—	
Missing	—	—	—		—	—	—	—	—	145.	145.
Total	—	—	274.	465.	2560.	226.	7.	—	—	145.	3677.

cus seems to bite at lower ranges of temperature and vapor pressure while *H. lucifer* bites in the higher ranges of these variables in the canopy. When the same ranges of temperature and vapor pressures are found near the floor of the forest, both of these insects are shown to engage in biting activity at that location.

To make comparisons of the space preferences of the most abundant species of man-biting insects, tables were prepared to show the percentage of the total of each species collected and the ambient air temperatures and vapor pressures at the time of the collection. When biting, the separation into regions of lower temperatures occupied by *Culicoides* and phlebotomines and higher temperatures occupied by the 2 species of mosquitoes is indicated in Table 5. There is some overlapping of the 2 regions but differentiation into separate regions is quite clear. The figure in the last column of the tables indicates the percentage of the total of each species collected in the given range of temperatures. For

Table 2.—Vapor pressure-temperature space, forest canopy station, 1974, *Culicoides diabolicus*.

Vapor pressure (millibars)	Temperature °C < 18.0	18.0 19.6	19.7 21.3	21.4 23.0	23.1 24.7	24.8 26.4	26.5 28.1	28.2 29.8	> 29.9	Missing	Total
< 22.4	—	—	250.	—	—	—	—	—	—	—	250.
22.4–23.3	—	—	251.	769.	—	—	—	—	—	—	1020.
23.4–24.3	—	—	15.	2580.	—	—	—	—	—	—	2595.
24.4–25.3	—	—	—	3839.	2688.	—	—	—	—	—	6527.
25.4–26.3	—	—	—	1976.	5399.	—	—	—	—	—	7375.
26.4–27.3	—	—	—	1119.	7640.	753.	—	—	—	—	9512.
27.4–28.3	—	—	—	—	9881.	85.	71.	—	—	—	10037.
28.4–29.3	—	—	—	—	4584.	7140.	—	—	—	—	11724.
29.4–30.3	—	—	—	—	1175.	2425.	—	—	—	—	3600.
30.4–31.3	—	—	—	—	—	75.	142.	—	—	—	217.
31.4–32.3	—	—	—	—	—	—	—	—	—	—	
32.4–33.3	—	—	—	—	—	—	—	—	—	—	
33.4–34.3	—	—	—	—	—	—	—	—	—	—	
34.4–35.3	—	—	—	—	—	—	—	—	—	—	
35.4–36.3	—	—	—	—	—	—	—	—	—	—	
36.4–37.3	—	—	—	—	—	—	—	—	—	—	
37.4–38.3	—	—	—	—	—	—	—	—	—	—	
38.4–39.3	—	—	—	—	—	—	—	—	—	—	
> 39.4	—	—	—	—	—	—	—	—	—	—	
Missing	—	—	—	—	—	—	—	—	—	198.	198.
Total	—	—	516.	10283.	31367.	10478.	213.	—	—	198.	53055.

Table 3.—Vapor pressure-temperature space, forest canopy station, 1974, *Haemagogus lucifer*.

Vapor pressure (millibars)	Temperature °C										
	< 18.0	18.0 19.6	19.7 21.3	21.4 23.0	23.1 24.7	24.8 26.4	26.5 28.1	28.2 29.8	> 29.9	Missing	Total
< 22.4	—	—	—	—	—	—	21.	—	—	—	21.
22.4–23.3	—	—	—	—	—	—	—	—	—	—	—
23.4–24.3	—	—	—	—	—	—	—	—	—	—	—
24.4–25.3	—	—	—	1.	—	1.	4.	—	1.	—	7.
25.4–26.3	—	—	—	3.	11.	3.	2.	—	—	—	19.
26.4–27.3	—	—	—	2.	1.	8.	27.	—	—	—	38.
27.4–28.3	—	—	—	—	8.	20.	24.	16.	40.	—	108.
28.4–29.3	—	—	—	—	23.	23.	13.	32.	13.	—	104.
29.4–30.3	—	—	—	—	—	32.	87.	20.	34.	—	173.
30.4–31.3	—	—	—	—	—	31.	65.	36.	32.	—	164.
31.4–32.3	—	—	—	—	—	16.	46.	9.	19.	—	90.
32.4–33.3	—	—	—	—	—	—	3.	15.	71.	—	89.
33.4–34.3	—	—	—	—	—	—	—	4.	—	—	4.
34.4–35.3	—	—	—	—	—	—	—	—	29.	—	29.
35.4–36.3	—	—	—	—	—	—	—	—	6.	—	6.
36.4–37.3	—	—	—	—	—	—	1.	2.	—	—	3.
37.4–38.3	—	—	—	—	—	—	—	—	—	—	
38.4–39.3	—	—	—	—	—	—	—	—	—	—	
> 39.4	—	—	—	—	—	—	—	—	—	—	
Missing	—	—	—	—	—	—	—	—	—	53.	53.
Total	—	—	—	6.	43.	134.	293.	134.	245.	53.	908.

example, in 1973, 97% of *C. diabolicus* were collected in the canopy when the temperatures were 21.4°–26.4°C, while during the same period 90% of *H. lucifer* were collected in the higher temperature range of 24.8°–29.9°C or higher. Table 6 in a similar manner indicates the separation into 2 regions of vapor pressure with the *Culicoides* and phlebotomines occupying the lower and the mosquitoes the higher vapor pressure regions. There is not quite so clear a separation into 2 regions as that indicated by the temperature variable.

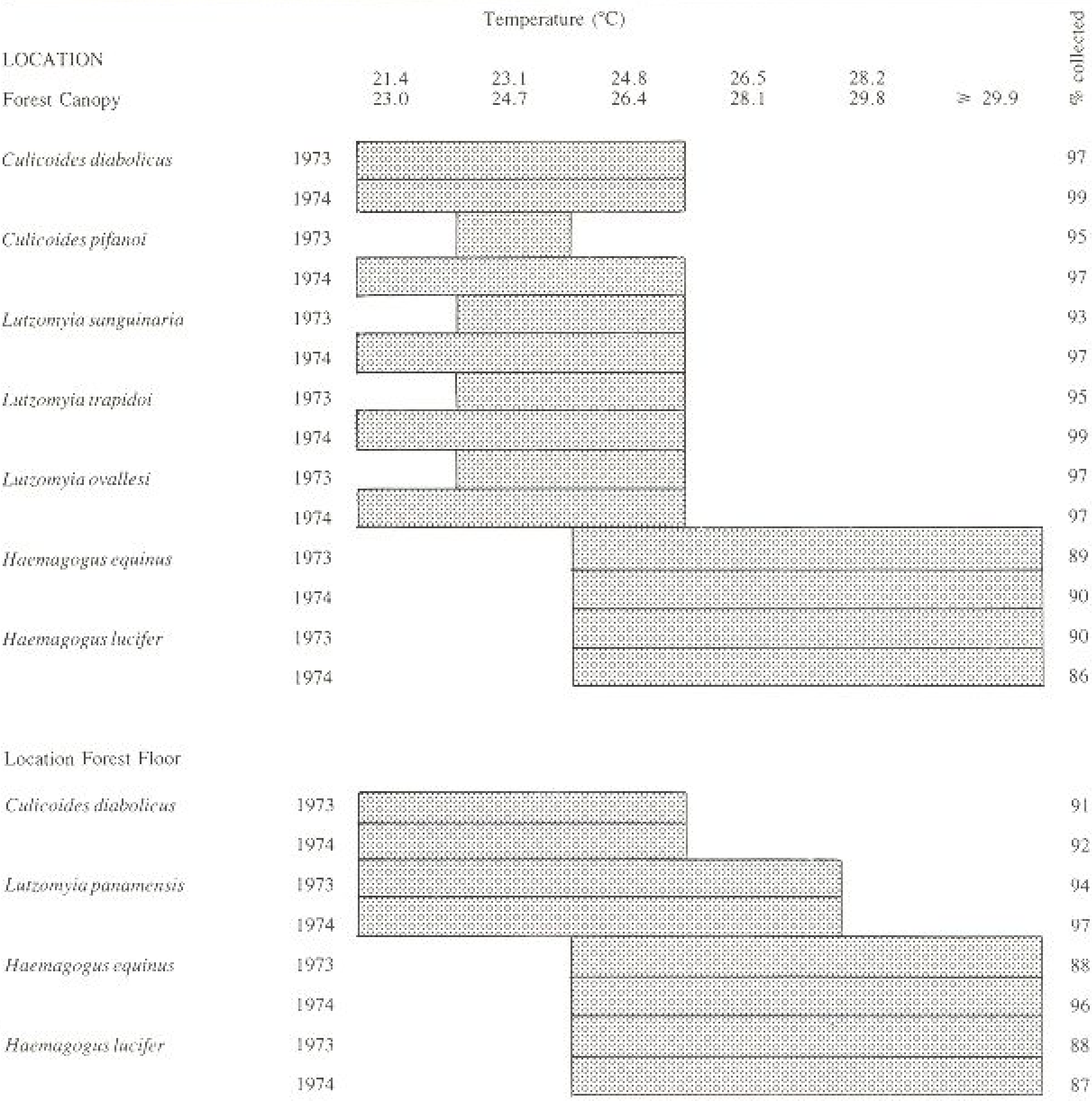
Discussion

It appears clearly from the data that these species of insects have a definite preference for a narrow range of temperature and humidity when engaged in biting activity. Temperature and vapor pressure were chosen because of

Table 4.—Vapor pressure-temperature space, forest floor station, 1974, *Haemagogus lucifer*.

Vapor pressure (millibars)	Temperature °C										
	< 18.0	18.0 19.6	19.7 21.3	21.4 23.0	23.1 24.7	24.8 26.4	26.5 28.1	28.2 29.8	> 29.9	Missing	Total
<22.4	—	—	—	—	—	1.	—	—	—	—	1.
22.4–23.3	—	—	—	—	—	4.	—	—	—	—	4.
23.4–24.3	—	—	—	2.	—	—	—	26.	—	—	28.
24.4–25.3	—	—	—	13.	—	—	2.	—	—	—	15.
25.4–26.3	—	—	—	—	18.	1.	—	—	—	—	19.
26.4–27.3	—	—	—	—	32.	4.	1.	9.	—	—	46.
27.4–28.3	—	—	—	—	23.	25.	4.	1.	2.	—	55.
28.4–29.3	—	—	—	—	—	10.	38.	17.	—	—	65.
29.4–30.3	—	—	—	—	—	56.	30.	1.	15.	—	102.
30.4–31.3	—	—	—	—	—	17.	73.	41.	3.	—	134.
31.4–32.3	—	—	—	—	—	31.	35.	31.	65.	—	162.
32.4–33.3	—	—	—	—	—	—	1.	10.	—	—	11.
33.4–34.3	—	—	—	—	—	—	7.	1.	35.	—	43.
34.4–35.3	—	—	—	—	—	—	—	—	—	—	
35.4–36.3	—	—	—	—	—	—	—	—	—	—	
36.4–37.3	—	—	—	—	—	—	—	—	—	—	
37.4–38.3	—	—	—	—	—	—	—	—	—	—	
38.4–39.3	—	—	—	—	—	—	—	—	—	—	
> 39.4	—	—	—	—	—	—	—	—	—	—	
Missing	—	—	—	—	—	—	—	—	—	32.	32.
Total	—	—	—	15.	73.	149.	191.	137.	120.	32.	717.

Table 5.—Air temperatures observed during insect collections at 2 levels in the forest showing the percentage of the total of each species collected in the range of temperatures indicated.

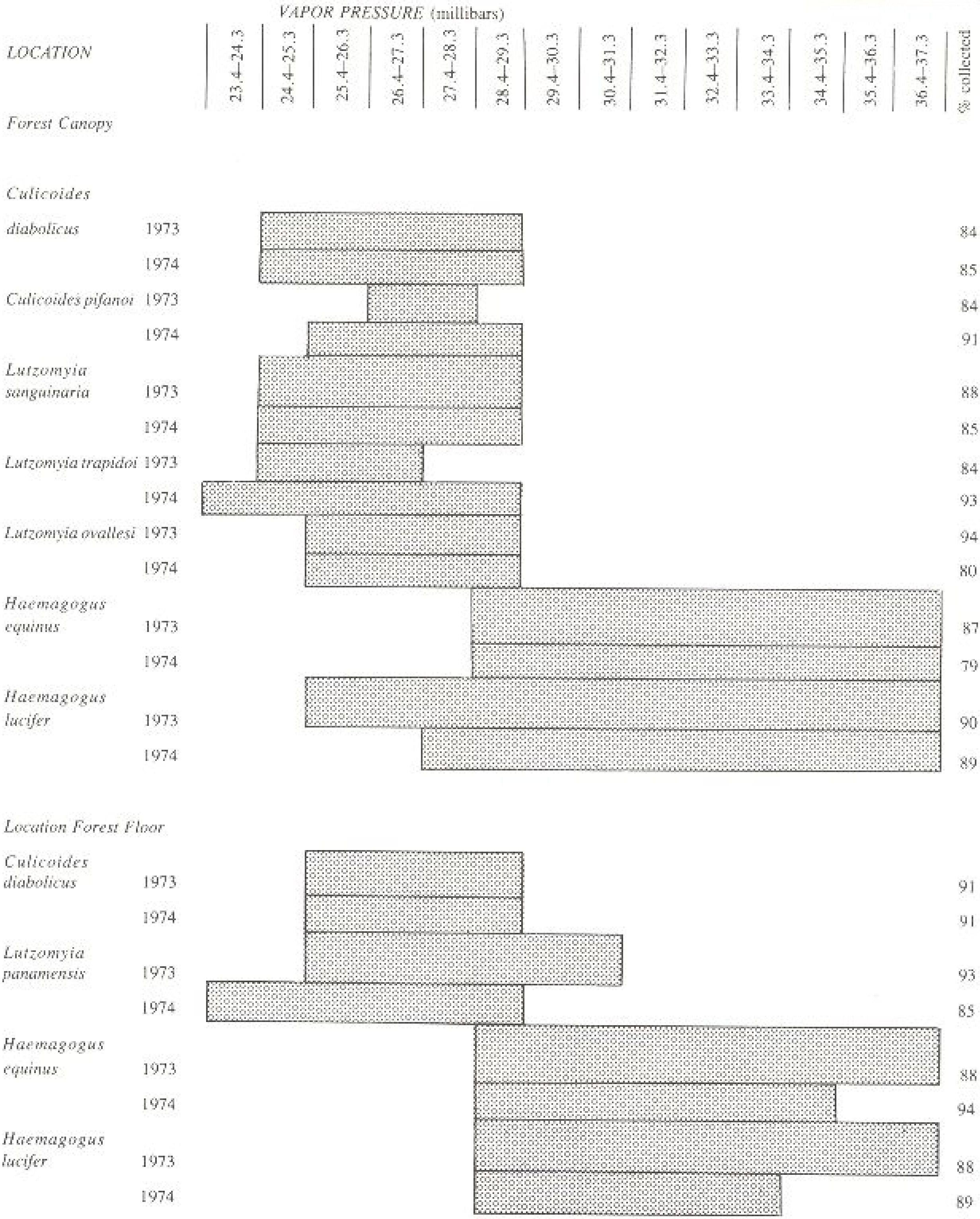


their importance as environmental factors regulating the heat exchange between the insect and the environment as well as the economy, ease, and reliability of these measurements. It is assumed that man-biting activity occupies only a small portion of the day-night period. The insect only becomes "visible" in this model when engaged in biting activity and thus remains "invisible" during much of any collection period.

It is often assumed that certain arthropods are daytime biters while others bite during the night, or in some cases the heaviest biting activity occurs in the period shortly before or following sunset. This model suggests that if the conditions of temperature and humidity are favorable, biting may occur at any time during the appropriate daily cycle for the species. Furthermore, as shown in Tables 5 and 6, there is an indication that if temperature and humidity are favorable the predominately canopy biters may migrate and bite near the ground.

The word "suggest" is used here because the temperature and vapor pressure are dependent on other atmospheric variables such as rainfall and wind. For example, when it rains heavily in the forest the ground temperatures may be lowered appreciably for hours or even days. This may cause low rates of evaporation in the forest, and both the air near the ground and in the canopy may be near saturation. During 1973 and 1974 the largest collections were made when

Table 6.—Vapor pressures observed during insect collections at 2 levels in the forest and the percentage of the total of each species collected in the range of vapor pressures indicated.



there was rain on the day before or on the day of collections. Winds may also cause changes in the stratification of temperature and humidity in the forest. During this same period the largest collections were made when wind speeds were less than 40 km/day (unpublished data.)

Conclusion

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 time. This model only describes the microhabitat of the studied species during biting activity in a natural forest environment. It does not suffer the drawbacks of describing a microhabitat in an artificial environment such as a laboratory colony.

The model presented 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.

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