THE AUTOECOLOGY OF THE ADULT HORN FLY, HAEMATORIA IRITANS (L.),
(DIPTERA: MUSCIDAE) ON DAIRY CATTLE

by

Neal Oliver Morgan

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TABLE OF CONTENTS

I. INTRODUCTION 8

II. REVIEW OF LITERATURE 10
   A. General 10
   B. Influence of weather on other arthropods 11
   C. Influence of weather on horn flies 16
   D. The influence of weather on insect physiology 17
   E. Ecological nomenclature 19

III. MATERIALS AND METHODS 21
   A. Macroclimatic measuring devices 21
   B. Microclimatic measuring devices 22
   C. Horn fly populations 26
      1. Biotopcs 26
      2. Method for taking horn fly census 27
      3. Methods for statistical analysis of data 28

IV. RESULTS AND DISCUSSION 29
   A. Macro-environment 29
      1. Definition 29
      2. Description of problem site 29
      3. Methods of measurement 30
      4. Data 32
         a. Cloud cover and horn flies 32
         b. Temperature 34
c. Humidity 41

d. Precipitation 41

e. Wind 47

5. Discussion 47

B. Micro-environment 52

1. Definition 52

2. Preparations for measurement 52

3. Methods of measurement 53

4. Data 54

   a. Temperature and light intensity 54

   b. Microhumidity 60

5. Discussion 60

V. CONCLUSIONS 71

VI. SUMMARY 73

VII. ACKNOWLEDGMENTS 76

VIII. BIBLIOGRAPHY 77

   A. Literature cited 77

   B. Literature not cited 83

IX. VITA 87
LIST OF TABLES

Table | Page
-----|------
1. Relation of the total horn fly populations on 10 test animals to the average high temperature for each week during the horn fly seasons of 1959 and 1960 | 38
2. Precipitation in excess of 0.5 inches during 48 hour periods and the apparent effect on contemporary horn fly populations | 46
3. Samples of data recorded during the 1960 horn fly season which indicate the effect of various wind velocities and macrotemperatures on horn fly populations | 48
4. Horn fly populations on windward and leeward sides of heifers at different wind velocities, macro-temperatures, and macrohumidities, 1960 | 49
5. Macrotemperatures and relative macrohumidities which occurred at seasonal peaks in average horn fly populations on the different breeds of heifers | 51
6. A comparison of mantle and skin temperatures and light intensity | 57
7. A comparison of skin temperatures of Holstein, Guernsey, and Jersey heifers at 3 selected macro-temperatures | 58
Table 8. A comparison of air temperatures within the mantle of Holstein, Guernsey and Jersey heifers at 3 selected macrotemperatures 59

9. Relative microhumidities of mantles of Holstein heifers observed during various relative macrohumidities 63

10. Relative microhumidities of mantles of Guernsey heifers observed during various relative macrohumidities 64

11. Relative microhumidities of mantles of Jersey heifers observed during various relative macrohumidities 65
LIST OF ILLUSTRATIONS

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Bendix-Fries psychron</td>
<td>25</td>
</tr>
<tr>
<td>2.</td>
<td>Tele-thermometer and 2 thermocouple probes</td>
<td>25</td>
</tr>
<tr>
<td>3.</td>
<td>Schematic aerial view of test area</td>
<td>31</td>
</tr>
<tr>
<td>4.</td>
<td>Relation of cloud cover to the average horn fly population for the different breeds, 1960</td>
<td>33</td>
</tr>
<tr>
<td>5.</td>
<td>Relation of weekly average number of horn flies per heifer to average macrotemperatures, 1959</td>
<td>35</td>
</tr>
<tr>
<td>6.</td>
<td>Relation of weekly average number of horn flies per heifer to average macrotemperatures, 1960</td>
<td>36</td>
</tr>
<tr>
<td>7.</td>
<td>Regression of horn fly population on weekly average minimum macrotemperatures</td>
<td>37</td>
</tr>
<tr>
<td>8.</td>
<td>Relation of horn fly population per breed (dark or light colored) of heifer for 5 selected macrotemperatures, 1959-1960</td>
<td>39</td>
</tr>
<tr>
<td>9.</td>
<td>Regression of horn fly population on weekly average maximum macrotemperatures</td>
<td>40</td>
</tr>
<tr>
<td>10.</td>
<td>Relation of average weekly minimum macrotemperature data for the horn fly seasons of 1959 and 1960 for Blacksburg, Virginia</td>
<td>42</td>
</tr>
<tr>
<td>11.</td>
<td>Number of horn flies per breed of heifer at 8 selected average daily relative macrohumidities, 1959-1960</td>
<td>43</td>
</tr>
<tr>
<td>12.</td>
<td>Regression of horn fly population on weekly average minimum relative macrohumidities</td>
<td>44</td>
</tr>
<tr>
<td>Figure</td>
<td>Page</td>
<td></td>
</tr>
<tr>
<td>--------</td>
<td>------</td>
<td></td>
</tr>
<tr>
<td>13. Regression of horn fly population on weekly average maximum relative macrohumidities</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td>14. Horn fly preference to black surface on a clear, warm day</td>
<td>56</td>
<td></td>
</tr>
<tr>
<td>15. Relation of horn fly populations to average skin temperatures of three breeds of heifers, 1960</td>
<td>61</td>
<td></td>
</tr>
<tr>
<td>16. Relation of horn fly populations to average air temperatures within the mantles of three breeds of heifers, 1960</td>
<td>62</td>
<td></td>
</tr>
<tr>
<td>17. Relation of horn fly populations to average relative microhumidities of the three breeds of heifers, 1960</td>
<td>66</td>
<td></td>
</tr>
<tr>
<td>18. Horn flies on white skin between the udder and hind leg of a Guernsey heifer during warm weather</td>
<td>69</td>
<td></td>
</tr>
</tbody>
</table>
I. INTRODUCTION

To the author's knowledge, the horn fly, *Haematobia irritans* L., has not been successfully cultured in the laboratory. Attempts to do so have resulted in either sterile adults being produced in the second generation or underdeveloped eggs being oviposited by the first generation females. Gravid female horn flies, after being collected in the field, oviposited fertile eggs. Young male and female horn flies collected in the field and maintained together in laboratory cages have not been observed to mate, and fertile eggs seldom have been obtained from them.

Many explanations have been offered for these results, namely, improperly designed diets for the adult flies, insufficient space for prenuptial flight, physically weak strains collected in the field, or wrong sex ratio. After many years of experimentation the problem has still not been completely solved. Harris (1962), however, has perfected a diet for maintaining horn flies in the laboratory without their feeding on animal hosts.

There is another approach to the problem, one which may eventually explain some of the weaker points of the previously mentioned ideas as well as indicate a missing element of the process for successful horn fly cultures. The approach involves a study of the micro- as well as the macro-environment of the horn fly. The macro-environment is defined as that concerning local atmospheric weather conditions, whereas the micro-environment is defined as that in which the horn fly
normally exists. (The micro-environment will be further defined as the problem develops.)

Perhaps there is a correlation between the environments which is requisite to normal sexual behavior of adult horn flies. Then, again, perhaps only one of environmental elements is necessary in the stimulation of normal sexual responses.

The purposes of this study are:

(a) to determine the optimum micro- and macro-environments for the adult horn fly;

(b) to note the conditions under which the adult populations increase, decrease, and become inactive, and;

(c) to define further the environmental factors controlling the adult horn fly populations.
II. REVIEW OF LITERATURE

A. General

The horn fly (*Haematobia irritans*, L.) apparently was first described by Linnaeus in 1758 (Bessi, 1907). It is now a well established pest of cattle in most countries of the New World from Venezuela to Canada and in the Old World from North Africa to Finland (Bessi, 1911 and Faisson, 1943). It is generally considered to be one of the most vexatious parasites of livestock wherever it occurs, and it is a more highly specialized parasite than is *Stomoxys calcitrans* (L.) which is less restricted in its movements and hosts (Glaser, 1923; McLintock and Depner, 1954).

Cattle are the principle hosts of the horn fly with the dark colored breeds being preferred over the lighter breeds. According to Bruce (1940) and Hammer (1941) adult flies do not travel any considerable distance under range conditions. The fly normally leaves its host only to deposit its eggs on freshly passed cattle dung, an operation that requires ten minutes at most (McLintock and Depner, 1957). Also, according to McLintock and Depner (1954), the stimuli which attract the flies to their hosts are unknown.

Until recently, fly infestations on cattle under range conditions consisted almost entirely of horn flies (Rogoff and Moxon, 1952). The damage caused by the flies is apparently due to the worry of the host, the loss of blood by the host, and the production of sores susceptible to screwworm attack (Bruce, 1940). According to Raun and Casey (1956)
horn flies reduce host weight-gains as much as one-half pound per day and milk production by 10 to 20% on cattle which are heavily infested with the flies.

The fly is capable of transmitting anthrax after biting an infected animal (Morris, 1918). Although anthrax is the only disease with which the horn fly has been associated, the role of the fly, if any, in the natural spread of the disease is still unknown.

In 1954, Mcintosh and Depner reported that horn fly mating had not been observed in cages. Glaser (1923) reported that first generation laboratory-reared adult female horn flies did not oviposit. Later, in 1924, he reported that his laboratory-reared first generation did not oviposit even though they lived for 24 days. Wild horn flies caught by him and brought into the laboratory, lived for 25 days, but they ceased oviposition 3 to 5 days after capture. Stirrat et al. (1955) concluded that one of the reasons for the failure of the flies to reproduce in the laboratory was the absence of some factor in the artificial environment that controls ovary development. Inasmuch as the common environment of the horn fly is apparently spatially limited to the surface of the host and fresh cattle dung, Hammer (1941) suggested that the host animal was surrounded by a mantle of high relative humidity preferred by the horn fly.

B. Influence of Weather on Other Arthropods

Mitchell and Epling (1951), working with Drosophila pseudo-obscura Meig., indicated that temperature, humidity and light were the
factors which possibly affected the feeding activity of the flies. According to them, the factors are interdependent and the reaction of the flies to each is quite different. Crewe and O'Rourke (1951) reported that the biting activity of *Chrysops silacea* Aust. increased with a rise in temperature and decreased with a rise in relative humidity, within the observed ranges.

Fales (1961) and Fales et al. (1961) stated that laboratory-reared face flies (*Musca autumnalis* DeGeer) become very active and the females readily oviposit after an hour or more exposure to actual or artificial sunlight. He further stated that specimens not exposed to such light either fail to oviposit or become sluggish.

Nicholson (1957) stated that any species adjusts its density in different places, and in the same place at different times, in relation to prevailing environmental conditions.

Weather is only one factor in the complex of interacting factors which limit the size a population can attain and continue to exist. The limit can be higher in one place than in another (Milne, 1959). Wider recognition of the existence of indirect effects of weather and climate could lead to a better understanding of the population dynamics of a species. Wellington (1954) stated, "With the concept of climatic release of a small indigenous population, wherein a species exists in small numbers and in which biotic conditions favor population growth, no initial increase may occur until seasonal climatic control is relaxed." Furthermore, according to him, favorable weather may have to recur several years in succession before a major increase in
population can develop.

Insects become acclimatized to different environmental temperatures very rapidly (usually within 24 hours), and acclimatization may alter their reactions at high and low temperatures. The effects of extreme temperatures may be substantially modified by a brief period of acclimatization (Mellanby, 1960). Colhoun (1954) however, suggested that acclimatization is only possible within a certain temperature range.

While studying insect habitats, Wellington (1950) noted that when rain fell, the difference between the temperature of the air and of the trees was negligible. However, as soon as the rain ceased, evaporation from rain drops resting on the foliage lowered the temperature of the trees as much as 2.8°F below that of the air for as long as 40 minutes. The observed differences between insect temperatures and the temperatures of the plants on which they fed, and the temperature of the surrounding air were sufficiently large to be given serious consideration in field studies. The differences observed were largely the result of radiant heating by day.

The appearance and abundance of horn flies, according to Marlatt (1910) is governed by temperature and rainfall. Buxton (1931) stated that it is generally understood that atmospheric humidity is often of great importance in limiting the times or places at which insects are abundant. Odum (1954) points out that the interaction of temperature and moisture depends on the relative as well as the absolute values of each factor. Temperature exerts a more retarding effect on
organisms when moisture conditions are extreme. Mellanby (1932) mentioned that relative humidity has no effect on the thermal death points of smaller insects providing the length of exposure is not greater than 1 hour.

El-Ziady (1958) on his study of a soft tick (Ornithodoros erraticus Lucas) indicated that light is of less importance than temperature and humidity in influencing the tick's behavior, and that temperature plays a more important role than does humidity. Dakshinamurty (1948), working with Musca domestica L., noted that low relative humidity was favorable to fly activity at high temperatures; however, at lower temperatures differences in relative humidity did not coincide with any marked differences in activity.

To show further the influence of temperature on insects, Holloway et al., in 1951, found that the rate of population increase for the Egyptian house fly was greatest when the mean temperature was between 20 and 25°C. Fly abundance dropped rapidly above 25°C but increased when the temperature fell below 25°C. Underhill (1941) indicated a definite relationship between the feeding of Simuliids and air temperature, whereby maximum feeding occurred when the temperature was between 75 and 85°F. According to Bursell (1960), the depth to which larvae of Glossina pallidipes Aust. burrow appears to be related to the temperature, and perhaps the humidity, present at the instant of larviposition. During cold weather, grasshoppers seek any shelter that offers a few degrees more warmth than the open air. If the ground temperature becomes too hot, they seek a preferable
temperature elsewhere (Parker, 1930).

No constant direct correlations are apparent between variations in numbers of *Anopheles quadrimaculatus* Say, and observed changes in the climatic conditions (Goodwin and Love, 1957). Increased humidity has a protective influence on the longevity of *Anopheles maculipennis* Meig. when the temperature is constant; however, at 80°F no amount of relative humidity can protect them for the full life span of one month. As the humidity increases during late summer, so does the population (Freeborn, 1932).

Underhill (1941) observed Simuliids feeding at relative humidities as low as 42% and as high as 98%. Apparently, humidity is not an important factor in the feeding of these insects.

Symmons (1959) indicated that there is a correlation between adult populations of red locusts and rainfall. Lea (1959) noted that a dry early summer "presaged" an increase in locusts during the following season, and a wet early summer "presaged" a decrease. Locust populations generally were low during the year following a year when the rainfall was above normal during the summer. Cool damp periods resulted in epidemics of diseases which greatly reduced locust populations. Scharff (1954) noted that outbreaks of grasshoppers occurred during or immediately following droughts, and low populations occurred when weather conditions were more humid.

It has been shown that the rate of development of certain insects is directly influenced by weather. Psairs (1927) stated that, within an insectary, temperatures which undergo daily variations similar to
outdoor temperature fluctuations have a more favorable effect on the rate of insect development than does a constant temperature.

C. Influence of Weather on Horn Flies

According to Bruce (1940) warm, damp, cloudy weather is the most favorable for horn fly development and, conversely, dry or cold weather is unfavorable. McLintock and Depner (1954) noted further that when the weather is cloudy or cool the flies always rest on the backs of the cattle. But when the weather is bright and warm, their resting place seems to depend on the air temperature. These investigators agreed with Hammer's (1941) suggestion that horn flies prefer an air temperature of about 37°C (98°F). Larsen (1943), however, reported that the upper temperature limit is 36°C (97°F).

Tesky (1960) suggested that the daily minimum temperatures influence the number of horn flies found on cattle. A rapid increase in numbers the first week of June of 1959 was halted a week later when the minimum temperatures fell from 59 to 39°F. The highest fly populations occurred when the minimum temperatures were between 50 and 65°F.

Apparently, coloration of the host or light intensity at the host's surface is a factor which influences the temperatures within the "mantle" of environment for the horn fly. Thomsen (1938) noted that the flies usually frequent the black areas of black and white cows by reason that the temperatures of such surfaces are undoubtedly higher than on the white surfaces. Also, he noted that the flies appear to seek shaded and sheltered places on the cattle. According
to Matthysee (1946) there is a noticeable difference between the skin temperature of a cow and the macrotemperature. He reported that on sunny days the black surfaces of cattle are as much as 3°F warmer than are the white surfaces. Mcintosh and Depner (1954) stated that hair temperatures differ according to the location on a cow and according to the local weather conditions. Using thermocouples, Thompsein et al. (1951) compared the skin and hair temperatures of dairy cattle with the temperatures of the surrounding air within a barn as well as outside. At about 0°F macrotemperature, the temperature difference between the skin and air was about 75°, between the hair and air about 45°, and between the hair and skin about 30°F. The temperatures tended to merge at 100 to 105°F macrotemperature.

Pratt (1912) noted that dry weather prevents horn fly larval development, but sudden and conspicuous increases in the adult horn fly populations occur following a period of frequent showers. Bruce and Eagleson (1938) found that in the laboratory horn flies thrive best in an environment of high relative humidity and require a continuous flow of fresh air. Bruce (1940) also noticed that the horn flies cluster on the shoulders and sides of the animals except when the weather was extremely hot or rainy when they tended to congregate on the undersides or the belly.

D. The Influence of Weather on Insect Physiology

Mellanby (1932) stated that heat regulation of an organism was influenced by the size of the organism. He theorized that heat taken
in by the body was proportional to the surface area of the body, and that evaporation was proportional to body volume. Therefore, a small animal is under great disadvantage in cooling itself and, when possible, seeks a favorable micro-environment. Also, according to him, relative humidity had no effects on the thermal death points of the smaller insects providing the length of exposure was limited to a few minutes. Beament (1945) proved that water loss was greatly accelerated when insects were subjected to temperatures above the melting points for the waxes of the epicuticle. Beattie (1928) believed that in air saturated with water, insects died at a lower temperature because they were unable to regulate their heat dissipation. Furthermore, he noted that the thermal death point of the blow fly (Phormia regina Meig.) was influenced by humidity and that dry air appeared to lower the thermal death point.

The range of temperatures within which insects are active is limited by the chill coma point (immobilization due to cold but not necessarily resulting in death) and the heat coma point (Hallanby, 1954).

Ballard (1958) concluded that both male and female Stomoxys calcitrana L. respond more readily to ultraviolet than to any other spectral region investigated. He indicated that it would be interesting to attempt to correlate such data with the spectral reflectance of dairy animals being heavily attacked by them. The activity of both sexes of stable flies decreased from the ultraviolet toward the greenish-yellow (550mm) to orange (620mm) where it was minimal.
E. Ecological Nomenclature

Terms are often misinterpreted in ecological papers, due probably to the vastness of the field and the number of contributors. However, many terms are of local origin and are ambiguous when used elsewhere. To prevent any misinterpretations of the ecological terms used in this paper, the following definitions are cited from Allee et al. (1940), Odum (1953) and Milne (1959).

**Abiotic environment:** the non-living environment composed of physical factors, i.e. sunlight, wind, rain, temperature, etc.

**Auteology:** the study of the individual organism or an individual species and its interrelations with the environment.

**Biocenose:** the total number of individuals of all the species living together in any region, as a community. This is governed by competition between species and is used in this paper to include the pasture containing the test animals.

**Biotope:** a microhabitat. Here it is extended to denote the mantle of micro-environment about the cow, in which the horn fly is believed to exist.

**Ecological action:** the effect of the abiotic environment on the population.

**Habitat:** the normal locus or residence of an organism.

**Population:** a group of individuals belonging to a single species.

**Population dynamics:** the change of size of a population during a period of time at a given place.
**Population ecology**: biodemography or the study of the relation of organisms (populations) to their environments. The term applies to a study of more than one species within an environment; whereas, autecology is limited to one species and its environment.

**Spatial distribution**: the differences in number of individuals from place to place at a given time.
III. MATERIALS AND METHODS

A. Macroclimatic Measuring Devices

Measurement of the field atmospheric temperature (macrotemperature) and relative humidity (macrohumidity) was achieved at two locations within the field containing the test animals by means of:

1) a semi-permanent weather station and 2) a portable tele-thermometer and portable psychrometer.

The semi-permanent station was composed of a rain gauge approved by the United States Department of Agriculture and a Bendix-Fries portable recording hygrothermograph. The latter was housed in a standard U. S. Weather Bureau instrument shelter, located on the terrain feature most completely exposed to air currents.

The accuracy of the hygrothermograph was compared with an instrument of the same model before the onset of each horn fly season and the adjustments were made accordingly. (The second instrument was standardized annually by a company-trained technician and was maintained by an employee of the U.S.D.A.) Daily comparisons were made in the field between the hygrothermograph and both the tele-thermometer and the psychrometer. No further adjustments were necessary.

The rain gauge was capable of measuring up to 6 inches (15 cm.) of precipitation with accuracy to 0.05 inches (1.25 mm.). The gauge was mounted on a post approximately 6 feet from the shelter containing the hygrothermograph. Precipitation was recorded, manually, every 24 hours during the rainy seasons as well as once each day the test
animals were examined. Correlation of the precipitation data with the macrotemperature and relative humidity data will be discussed later.

The entire weather station was enclosed within a 5-strand barbed wire fence which prohibited the test heifers from standing closer than 5 feet to the instrument shelter. The heifers seldom approached within 30 feet of the station due, in part, to the lack of water or vegetation in the immediate vicinity.

B. Microclimatic Measuring Devices

Measurement of the microhumidity necessitated the use of a portable, electrically aspirated psychrometer. Thus, a Bendix-Fries Psychron (Fig. 1), was employed for three reasons:

(1) The intake aperture was so designed as to enable relative microhumidity measurements with the wet and dry bulb thermometers being within 0.25 inches (0.625 cm.) from the animal surface. (2) The accuracy of the wet and dry bulb thermometers was within 0.2°F in the range of +15° to +90° and within 0.3°F for 10° above and below the same range.

(3) It was a handy size for use around animals in the field. The complete unit with two dry-cell batteries weighed 2.5 pounds, measured approximately 2.5 inches (6.25 cm.) wide by 10 inches (25 cm.) long by 5 inches (12.5 cm.) high, and its motor was sufficiently quiet so as not to terrify halter-broken animals.

The animals used for the study were Holstein, Jersey and Guernsey
yearling heifers. Introduction of the psychrometer and the sound of its motor to the heifers was a minor problem which had to be eliminated before accurate data could be recorded about the animals. Normally, heifers became nervous when unfamiliar objects were brought near them or when they heard unusual sounds. Not only was the psychrometer new to the heifers, but the instrument was operated by a motor the noise of which closely resembled that of adult cattle grubs (*Hypoderma spp*). Before introducing any new instruments or techniques to the test animals, the animals were haltered and tied to trees or strong fence posts. By permitting the animals to smell and examine the psychrometer with the motor "on" and "off" and by permitting them to watch the operator move the instrument over their bodies the animals became adjusted to its presence, usually within the first week of operation. By mid-season many of the heifers permitted examination with the psychrometer without being haltered.

To obtain the microhumidity data, the air intake aperture was positioned parallel to and approximately 0.25 inches (0.625 cm.) from the skin surface of the test animal. After the psychrometer was turned on, the wet and dry bulb thermometers were allowed to stabilize and the temperatures were recorded. Wind velocity had the greatest influence on the rate of stabilization which usually occurred within 30 seconds. The translations (per cent relative humidity) were computed from a psychrometric slide rule which was furnished with the instrument.

Temperatures were recorded at the skin surface and at 0.25, 0.5,
1.0 and 2 inches from the surface of each animal. The determination of near instantaneous temperature readings at such locations necessitated the use of thermocouple probes and a tele-thermometer (Fig. 2). The instrument and the probes were manufactured by the Yellow Springs Instrument Company, Yellow Springs, Ohio, and were employed for reasons similar to those listed for the portable psychrometer. They were as follows:

1. The unit was easily portable. The tele-thermometer measured approximately 3 by 5 by 7.5 inches, weighed about 2 pounds complete with one dry-cell battery. By using the thermocouple probes on 8-foot extensions, all areas to be examined about a heifer were easily reached without exposing the sensitive instrument to the curiosity of cantankerous test animals.

2. The dial was calibrated in both Fahrenheit and Centigrade scales with the increments of the Fahrenheit scale being 2° and of the Centigrade scale 1°.

3. The indicator needle registered accurate temperatures usually within 30 seconds.

Two types of probes were employed; one was a surface temperature probe - a stainless steel wafer 0.40625 inch in diameter and 0.0625 inch thick with a time constant of 0.8 seconds. The wafer was attached to the 8-foot extension by a 3.1875 inch piece of 17-gauge stainless steel wire. The probe was small enough to be placed against the skin of a heifer without clipping the hair from the area.

The second type of probe, an air temperature probe also of stain-
Figure 1. Bendix-Friez psychron

Figure 2. Tele-thermometer and 2 thermocouple probes
less steel, was a heat sensitive element within a steel cage. The
time constant of the element was 2 minutes in free, still air. The
protective cage was 0.5 inch in diameter and 0.59375 inch long. The
surface of the heat sensitive element was 0.25 inches from the opened
end of the cage; hence, a temperature reading could be obtained from
0.25 inches of a surface.

C. Horn Fly Populations

1. Biotopes

According to McLintock and Depner (1957), the biotope of the
horn fly is limited to the surface of the animal host. Also, accord-
ing to them, the female fly leaves the biotope only to oviposit on
freshly passed cattle dung, a round trip that seldom requires 10 min-
utes to complete. Therefore, it is evident that the majority of the
adult fly life occurs on the animal host.

An accurate census of the adult horn fly population within a
biocenose requires counting all the horn flies in all of the biotopes,
on the fresh cattle dung piles, and along all the air routes traveled
by the flies. Such accuracy was not feasible for this investigation.
Only those horn flies which are in the biotopes being examined for
micro-environmental data are counted for the census.

The distribution of the flies on each animal host differs for
no two biotopes have the same surface areas nor identical areas and
amounts of coloration. As Hearle (1938) and Bruce (1940) indicated,
horn flies are more commonly attracted to dark colored surfaces than to white. However, Hammer (1941) noted that on hot, clear days the horn flies tended to cluster on protected white surfaces of cows, such as the navel or between the udder and the hind leg.

For this investigation a herd of dairy heifers was maintained in a pasture. Each year, the herd was comprised of 24 to 27 Holstein, 13 to 17 Jersey and 9 to 10 Guernsey heifers.

2. Method for Taking Horn Fly Census

Ten animals were randomly selected from the herd for daily examination with the number of each breed selected being proportional to the breed composition of the herd. Thus, 5 Holstein, 3 Jersey, and 2 Guernsey heifers were examined each day.

All of the horn flies were counted and their locations on each animal were noted in relation to the color of the surface of the skin and the location on the animal relative to such landmarks as belly, mid-line, flank, or spine. The information was later combined with microclimatical data obtained from the same areas in an effort to determine the micro-environmental conditions sought by the flies.

During the preliminary census of the first season, only the flies on one side of each animal were counted and later multiplied by 2 for a total for the animal; however, further observations indicated gross inaccuracies by such procedures. Depending on many factors discussed elsewhere in this paper, the flies could all be resting on one side or on the belly of the animal, and the census taker would record
zero flies for an animal actually supporting several hundred.

3. Methods for Statistical Analysis of Data

The method employed for statistical analysis was simple linear regression and was calculated by an International Business Machines computer (Model 650), operated by the Statistics Department staff at Virginia Polytechnic Institute. The following relationships were analysed:

(1) The effects on horn flies by dark and light colored skin.
(2) High and low macrotemperature.
(3) High and low relative humidity.
(4) Rainfall.
IV. RESULTS AND DISCUSSION

A. Macro-environment

1. Definition

The environment of the biocenose beyond the approximately 0.5 inches thick mantle encompassing the animal host is referred to as the macro-environment. It is further limited to the general area in which the host is located. In this case it is the area within the normal flight radius of the horn fly. It is influenced by several abiotic factors among which are the amount of sunlight, direction and velocity of wind, temperature, humidity, and precipitation. The actual influence on the horn fly population appears to result from coordinated effects of these factors.

2. Description of Problem Site

During the 2 years of investigation, all phases of measurement were accomplished in the same pasture, adjacent to the town of Blacksburg, Virginia. The pasture was an irregularly shaped area of 43.5 acres, a part of the pasturage for the dairy herd at Virginia Polytechnic Institute. The area was located south of the town limits and was relatively isolated from neighboring herds of cattle. The east border of the pasture was separated from a paved highway (U. S. Route 460) by 30 feet of uncultivated right-of-way. Beyond the highway and a like distance from same was a similar herd of V.F.I. heifers,
which occasionally were observed to corroborate data of the test herd. North and west of the test pasture, the nearest cattle were a minimum of 1 mile away and south approximately 0.5 mile away. The pasture was located on the crest and eastern slope of the eastern continental divide (Fig. 3).

The topography of the area was of gently rolling hills, interrupted by 3 natural springs with all of the water courses flowing from approximately west to east. The terrain elevations varied from 2016 to 2082 feet above sea level.

The prevailing winds were from the northwest and seldom during the two fly seasons were wind velocities recorded above 35 miles per hour.

3. Methods of Measurement

The macro-environment is dynamic, changing continually throughout the daylight hours according to the position of the sun relative to the test area. Heat or light intensity, humidity and air-motion are simultaneously affected. Therefore, all measurements of the macro-environment were recorded within 5 minutes preceding the recording of micro-environmental data on the randomly selected test animals.

The temperature and humidity data were read directly from a recording hygrothermograph, however the light intensity data were less readily obtainable. Rather than using a photographer's light meter and measuring the light reflected from several objects in the area and attempting to interpret such data, the amount of cloud cover was
Figure 3. Schematic aerial view of test area.
recorded. The data for each day were interpreted in toto for future comparisons. The terms employed for recording cloud cover are:

1. **Ground fog**
2. **Overcast** (solid cloud cover)
3. **Cloudy** (with small patches of blue sky showing)
4. **Moderately cloudy** (half clouds and half clear sky showing)
5. **Partly cloudy** (small clouds sparsely scattered)
6. **Clear**

Air motion was not measured with an instrument, rather it was estimated at the time of each examination. Air speed was estimated to an accuracy of ± 5 miles per hour. The direction of the wind was, also, estimated with the use of a vane within a few hundred yards of the pasture and was recorded according to the 8 major points of the compass. Comparison of the estimated data with the data of corresponding dates, as published in the U. S. Department of Commerce monthly weather survey for the state of Virginia, indicated that the estimates were reasonably correct.

4. **Data**

a. **Cloud Cover and Horn Flies**

The effects of cloud cover or sunlight appear to have little influence on the population of horn flies on individual heifers (Fig. 4); instead, as will be further discussed, the combination of cloud cover plus macrotemperature and macrowumidity influence the
Figure 4. Relation of cloud cover to the average horn fly population for the different breeds, 1960.

Ground fog  Overcast  Cloudy  Mod. cloudy  Partly cloudy  Clear

H = Holstein
G = Guernsey
J = Jersey
general location of horn flies within the biotope. For example, during a cold and fog bound period, the majority of horn flies usually are found along the belly midlines of standing heifers or on protected surfaces as the skin between the hind leg and the udder or belly of prone animals. For each condition of cloud cover the difference in fly populations is more noticeable between breeds of heifers than between individuals of one breed. During the 1960 horn fly season the overcast, partly cloudy, and clear conditions each prevailed for approximately 25% of the daily observations.

b. Temperature

Many authors (Marlatt, 1910; Hearle, 1938; Bruce, 1940; Hammer, 1941; Bogoff and Moxon, 1952; and McIntock and Depner, 1954) have previously stated that the greatest horn fly populations occur in this hemisphere during the mid-summer months. Also, some authors surmised that the increase in populations was directly influenced by the increase in seasonal heat. The data obtained during the horn fly seasons of 1959 and 1960 indicate that seasonal heat is a primary factor insomuch as it influences horn fly population and relative humidities (Figs. 5, 6 and 7). However, according to simple linear regression analysis, the relation between horn fly populations on the entire herd and high temperatures is not significant at the 5% level (Table 1 and Figs. 8 and 9).

Although the maximum macrotemperatures for May, early June, and early October were warm enough during 1959 and 1960 to sustain
Figure 5. Relation of weekly average number of horn flies per heifer to average macro-

temperatures, 1959.

Temperature in degrees Fahrenheit

- 35 -
Figure 6. Relation of weekly average number of horn flies per heifer to average macro-temperatures, 1960.
Figure 7. Regression of horn fly population on weekly average minimum macrotemperatures. Each dot represents the average horn fly population per animal for the selected minimum temperatures during the horn fly seasons of 1959 and 1960, Blacksburg, Virginia. (Highly significant at the 1% level.)

\[ b = 5.6513 \]
Table 1. Relation of the total horn fly populations on 10 test animals to the average high temperature for each week during the horn fly seasons of 1959 and 1960.

<table>
<thead>
<tr>
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<th></th>
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</thead>
<tbody>
<tr>
<td>1 (May 6)</td>
<td>1918</td>
<td>84</td>
<td>1 (May 10)</td>
<td>276</td>
<td>65</td>
</tr>
<tr>
<td>2</td>
<td>2034</td>
<td>64</td>
<td>2</td>
<td>684</td>
<td>80</td>
</tr>
<tr>
<td>3</td>
<td>1840</td>
<td>75</td>
<td>3</td>
<td>1116</td>
<td>75</td>
</tr>
<tr>
<td>4</td>
<td>3570</td>
<td>76</td>
<td>4</td>
<td>1575</td>
<td>80</td>
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<tr>
<td>5</td>
<td>1504</td>
<td>72</td>
<td>5</td>
<td>1704</td>
<td>77</td>
</tr>
<tr>
<td>6</td>
<td>2134</td>
<td>82</td>
<td>6</td>
<td>1944</td>
<td>82</td>
</tr>
<tr>
<td>7</td>
<td>2396</td>
<td>72</td>
<td>7</td>
<td>2634</td>
<td>78</td>
</tr>
<tr>
<td>8</td>
<td>2923</td>
<td>84</td>
<td>8</td>
<td>2130</td>
<td>82</td>
</tr>
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<td>11</td>
<td>5380</td>
<td>79</td>
<td>11</td>
<td>3741</td>
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<td>13</td>
<td>9650</td>
<td>84</td>
<td>13</td>
<td>3973</td>
<td>90</td>
</tr>
<tr>
<td>14</td>
<td>9850</td>
<td>78</td>
<td>14</td>
<td>4048</td>
<td>81</td>
</tr>
<tr>
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<td>9180</td>
<td>81</td>
<td>15</td>
<td>4398</td>
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<td>16</td>
<td>10550</td>
<td>85</td>
<td>16</td>
<td>4119</td>
<td>79</td>
</tr>
<tr>
<td>17</td>
<td>7174</td>
<td>87</td>
<td>17</td>
<td>3113</td>
<td>87</td>
</tr>
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<td>5686</td>
<td>78</td>
<td>18</td>
<td>4035</td>
<td>80</td>
</tr>
<tr>
<td>19</td>
<td>1482</td>
<td>76</td>
<td>19</td>
<td>2778</td>
<td>75</td>
</tr>
<tr>
<td>20 (Sept. 26)</td>
<td>4275</td>
<td>70</td>
<td>20</td>
<td>3114</td>
<td>71</td>
</tr>
<tr>
<td>21</td>
<td></td>
<td></td>
<td>21</td>
<td>2739</td>
<td>73</td>
</tr>
<tr>
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<td></td>
<td>22</td>
<td>2550</td>
<td>75</td>
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<td>23</td>
<td></td>
<td></td>
<td>23</td>
<td>1012</td>
<td>64</td>
</tr>
<tr>
<td>24 (Oct. 24)</td>
<td></td>
<td></td>
<td></td>
<td>95</td>
<td>52</td>
</tr>
</tbody>
</table>

Regression value \( F_{1,453} = 3.8484 \)

Not significant at the 5% level.
Figure 3. Relation of horn fly population per breed (dark or light colored) of heifer for 5 selected macrotemperatures, 1959-1960.
Figure 9. Regression of horn fly population on weekly average maximum macrotemperatures. Each dot represents the average horn fly population per animal for the selected maximum temperatures during the horn fly seasons of 1959 and 1960, Blacksburg, Virginia. (Not significant at the 5% level.)

\[ b = -2.2054 \]
horn fly populations, the minimum temperatures were so low as to inhibit horn fly activity (Figs. 7 and 10).

c. Humidity

According to the data in Figures 8 and 11, the black breed (Holstein) attracts more horn flies than do the brown breeds. Furthermore, the greatest horn fly populations coincided with macrohumidities ranging from a daytime minimum of 40% to a nighttime maximum of 88% (Fig. 11). During periods of low macrohumidity (below 40%) the data indicated that the horn fly populations appeared to increase slightly (Fig. 12). Also, during periods of high macrohumidity (above 88%) the data indicated that the adult horn fly populations appeared to decrease (Fig. 13).

d. Precipitation

During dry, warm weather horn flies appeared to prefer the colored regions of skin on Holstein and Guernsey heifers. However, during periods of precipitation ranging from ground fog to heavy showers, the horn flies either moved to protected areas regardless of the skin coloration or they burrowed deeper between the hairs. Precipitation accompanied by breezes from one direction usually caused noticeable movement of the horn flies from the exposed to the more protected areas on the lee side or belly of the animal. Rainfall tended to reduce the horn fly population when the amount of precipitation measured greater than 0.5 inches during 48 hour periods (Table 2).
Figure 10. Relation of average weekly minimum macrotemperature data for the horn fly seasons of 1959 and 1960 for Blacksburg, Virginia.
Figure 11. Number of horn flies per breed of heifer at 8 selected average daily relative
Figure 12. Regression of horn fly population on weekly average minimum relative macro-
humidities. Each dot represents the average horn fly population per animal 
for the selected minimum relative humidities during the horn fly seasons of 
1959 and 1960, Blacksburg, Virginia. (Highly significant at the 1% level.)
Figure 13. Regression of horn fly population on weekly average maximum relative humidity. Each dot represents the average horn fly population per animal for the selected relative humidities during the horn fly seasons of 1959 and 1960, Blacksburg, Virginia. (Significant at the 5% level.)
Table 2. Precipitation in excess of 0.5 inches during 48 hour periods and the apparent effect on contemporary horn fly populations. The macrotemperature was measured when the post-storm fly census was taken.

<table>
<thead>
<tr>
<th>Precipitation</th>
<th>Av. population per animal</th>
<th>Macrot</th>
<th>Decrease</th>
<th>Pct.</th>
<th>°F</th>
</tr>
</thead>
<tbody>
<tr>
<td>in.</td>
<td>Pre-storm</td>
<td>Post-storm</td>
<td>Temperature</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1959</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.58</td>
<td>50.7</td>
<td>40.7</td>
<td>17.8</td>
<td>74</td>
<td></td>
</tr>
<tr>
<td>0.60</td>
<td>185.0</td>
<td>165.0</td>
<td>10.8</td>
<td>84</td>
<td></td>
</tr>
<tr>
<td>0.60</td>
<td>165.0</td>
<td>142.5</td>
<td>13.6</td>
<td>89</td>
<td></td>
</tr>
<tr>
<td>0.62</td>
<td>48.1</td>
<td>27.1</td>
<td>43.6</td>
<td>66</td>
<td></td>
</tr>
<tr>
<td>0.66</td>
<td>200.0</td>
<td>132.5</td>
<td>33.7</td>
<td>80</td>
<td></td>
</tr>
<tr>
<td>0.74</td>
<td>65.4</td>
<td>48.1</td>
<td>26.45</td>
<td>66</td>
<td></td>
</tr>
<tr>
<td>0.84</td>
<td>115.2</td>
<td>81.2</td>
<td>29.51</td>
<td>74</td>
<td></td>
</tr>
<tr>
<td>1.90</td>
<td>165.0</td>
<td>150.0</td>
<td>9.09</td>
<td>76</td>
<td></td>
</tr>
<tr>
<td>2.21</td>
<td>81.2</td>
<td>50.7</td>
<td>37.56</td>
<td>78</td>
<td></td>
</tr>
<tr>
<td>1960</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.62</td>
<td>74.2</td>
<td>72.7</td>
<td>2.02</td>
<td>63</td>
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<tr>
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<td>127.2</td>
<td>7.8</td>
<td>93.87</td>
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</tr>
<tr>
<td>0.72</td>
<td>258.0</td>
<td>181.1</td>
<td>29.81</td>
<td>87</td>
<td></td>
</tr>
<tr>
<td>0.78</td>
<td>242.2</td>
<td>106.0</td>
<td>56.23</td>
<td>66</td>
<td></td>
</tr>
</tbody>
</table>

Regression value \( F_{1,453} = 4.6778 \)

Significant at the 5% level.
This was especially true at low temperatures.

e. Wind

Wind velocity of less than 20 miles per hour apparently has negligible effect on the size of horn fly populations (Tables 3 and 4). Although velocity in excess of 20 m.p.h. appeared to deplete horn fly populations; this depletion often occurred during periods of adverse macrotemperature and/or macrohumidity. Thus, sustained high winds caused depletion of horn fly populations regardless of the macrotemperature or macrohumidity. Cold or wet weather appeared to be intensified by the wind, and this incited immediate movement of the horn flies to the more protected areas of the hosts.

5. Discussion

The horn fly population within a biocenose is apparently dependent upon the coordinated influences of the 4 forces of the macroclimate, namely sunlight, temperature, relative humidity, and wind.

Cloud cover appears to have little effect in directly controlling horn fly populations; however, the distribution of flies within a biotope is often influenced by sunlight. As will be elucidated later, on cloudless days horn flies prefer dark colored hosts. During the periods when the light intensity is low or while there are cloudy conditions, the horn flies tend to be more evenly distributed between the 3 breeds of heifers. The difference between horn fly populations on brown cattle and those on black and white cattle is apparently
Table 3. Samples of data recorded during the 1960 horn fly season which indicate the effect of various wind velocities and macrotemperatures on horn fly populations.

<table>
<thead>
<tr>
<th>Wind Direction</th>
<th>Velocity mph</th>
<th>Macrotemperature °F</th>
<th>Average horn fly population</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>5</td>
<td>92</td>
<td>107.0</td>
</tr>
<tr>
<td>N</td>
<td>5</td>
<td>76</td>
<td>350.0</td>
</tr>
<tr>
<td>N</td>
<td>20</td>
<td>79</td>
<td>96.0</td>
</tr>
<tr>
<td>NW</td>
<td>35</td>
<td>52</td>
<td>1.8</td>
</tr>
<tr>
<td>W</td>
<td>5</td>
<td>84</td>
<td>126.7</td>
</tr>
<tr>
<td>W</td>
<td>5</td>
<td>74</td>
<td>176.5</td>
</tr>
<tr>
<td>W</td>
<td>15</td>
<td>83</td>
<td>139.0</td>
</tr>
<tr>
<td>W</td>
<td>20</td>
<td>78</td>
<td>138.0</td>
</tr>
<tr>
<td>W</td>
<td>25</td>
<td>81</td>
<td>83.9</td>
</tr>
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<td>W</td>
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<td>90.5</td>
</tr>
<tr>
<td>S</td>
<td>5</td>
<td>85</td>
<td>166.0</td>
</tr>
<tr>
<td>S</td>
<td>5</td>
<td>74</td>
<td>302.0</td>
</tr>
<tr>
<td>-</td>
<td>0</td>
<td>68</td>
<td>140.9</td>
</tr>
<tr>
<td>-</td>
<td>0</td>
<td>52</td>
<td>82.5</td>
</tr>
</tbody>
</table>
Table 4. Horn fly populations on windward and leeward sides of heifers at different wind velocities, macrotemperatures, and macrohumidities, 1960.

<table>
<thead>
<tr>
<th>Wind velocity</th>
<th>Average fly population per animal side</th>
<th>Macrotemperature</th>
<th>Relative humidity</th>
</tr>
</thead>
<tbody>
<tr>
<td>mph</td>
<td>Windward</td>
<td>Leeward</td>
<td>°F</td>
</tr>
<tr>
<td>0</td>
<td>171</td>
<td>190</td>
<td>70</td>
</tr>
<tr>
<td>5</td>
<td>82</td>
<td>89</td>
<td>74</td>
</tr>
<tr>
<td>5</td>
<td>176</td>
<td>9</td>
<td>64</td>
</tr>
<tr>
<td>5</td>
<td>267</td>
<td>83</td>
<td>76</td>
</tr>
<tr>
<td>5</td>
<td>600</td>
<td>4</td>
<td>79</td>
</tr>
<tr>
<td>20</td>
<td>41</td>
<td>55</td>
<td>79</td>
</tr>
</tbody>
</table>
less only during the early part of the horn fly season. Then the minimum daily macrotemperature is not warm enough to induce emergence of large numbers of adults or oviposition by mature female horn flies. In addition, the intensity of sunlight determines the rate and extent of macrohumidity and macrotemperature fluctuation during the daylight hours.

Precipitation is of consequence to the hornflies when it is either over-abundant or when the macrotemperature is below 50°F. Heavy rains apparently not only drown newly emerged flies but tend to decimate the horn fly population within each biotope when the host is fully exposed to the storm.

As will be further elaborated later, most horn flies will withstand temperatures beyond the maximum of 97°F. as reported by Hammer (1941), but only when the relative macrohumidity or a microhumidity is above 50%, the air movement is slow, and the flies are on the colored areas of the hosts. The approximate optimum day and night temperatures for horn flies or the average of the temperatures that coincided with the peaks of horn fly incidence in 1959 and 1960 are 77° and 76°F, respectively (Table 5). The approximate optimum relative macrohumidity range for the horn fly is from a daytime low of 40% to a nighttime high of 90% and a mean of 65% (Table 5 and Figures 11, 12, and 13).
Table 5. Macrotemperatures and relative macrohumidities which occurred at seasonal peaks in average horn fly populations on the different breeds of heifers.

<table>
<thead>
<tr>
<th></th>
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<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Temperature</td>
<td>Relative humidity</td>
<td></td>
<td></td>
<td>Temperature</td>
<td>Relative humidity</td>
<td></td>
</tr>
<tr>
<td>Holstein</td>
<td>Minimum</td>
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<td>44</td>
<td>300</td>
<td>66</td>
<td>42</td>
<td>344</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>77</td>
<td>67</td>
<td></td>
<td>76</td>
<td>66</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>88</td>
<td>89</td>
<td></td>
<td>86</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Guernsey</td>
<td>Minimum</td>
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<td>36</td>
<td>220</td>
<td>62</td>
<td>43</td>
<td>173</td>
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<tr>
<td></td>
<td>Average</td>
<td>77</td>
<td>62</td>
<td></td>
<td>71</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>86</td>
<td>88</td>
<td></td>
<td>80</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Jersey</td>
<td>Minimum</td>
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<td>36</td>
<td>195</td>
<td>62</td>
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<td>151</td>
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<tr>
<td></td>
<td>Average</td>
<td>77</td>
<td>62</td>
<td></td>
<td>72</td>
<td>76</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>86</td>
<td>88</td>
<td></td>
<td>82</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Combined</td>
<td>Minimum</td>
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<td>36</td>
<td>252</td>
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<td>Average</td>
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<td>62</td>
<td></td>
<td>72</td>
<td>76</td>
<td></td>
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<tr>
<td></td>
<td>Maximum</td>
<td>86</td>
<td>88</td>
<td></td>
<td>82</td>
<td>90</td>
<td></td>
</tr>
</tbody>
</table>
B. Micro-environment

1. Definition

Many insects have an optimum combination of temperature and humidity, both for survival and development (Allee et al., 1949). As Milne (1957) stated, every species within its distributional range occupies not all habitats but only those where conditions are suitable. The adult horn fly occupies a biotope or habitat wherein the micro-environment is suitable, namely, on the surface of either a dairy or beef animal. Therefore, the micro-environment for the horn fly is that environment which occurs within a 0.5 inch (1.25 cm.) thick mantle which encompasses the host animal and includes the surface of the same. The micro-environment is as dynamic and almost as flexible as is the macro-environment.

As Allee et al. (1949) indicate, the minor niches within major biotic formations have their own distinctive microclimates, with their own seasonal cycles, and aggregations result from reactions to various gradients of environmental forces. Every change in the position of the host animal during the daylight hours causes modifications of the microclimate within the mantle.

2. Preparations for Measurement

Before attempting to determine the microclimatical conditions within the mantle of each test animal, the 10 randomly selected heifers were haltered and tethered to fence or hitching posts. The location
of the post was determined usually less than 5 minutes before the animals were haltered with the proposed tethering posts being as completely exposed to sunlight and air currents as possible yet remaining within the test pasture. The animals not haltered often attempted to mingle with the others and disturb the horn fly populations; hence, immediately before examining the test heifers the remainder of the herd were discouraged from remaining within 30 to 40 feet of the examination site.

Before the horn fly seasons commenced, new dry cell batteries were installed in the psychrometer and tele-thermometer. Also, prior to each daily examination period, the 2 meters were operated in the laboratory to observe their responses to the predetermined laboratory conditions and to estimate the condition of the dry cell batteries.

In the field, as mentioned earlier, the instruments were operated beside the weather station to permit a comparison between their measurements and those recorded by the hygrothermograph.

3. Methods of Measurement

Temperature and humidity were recorded for 4 loci on the body of each test heifer; (1) along the spine, (2) sunlit flank, (3) shaded flank, and (4) belly. Of the bicolored animals, data were recorded for each color at the four regions. Notes were made on any abnormally large populations of horn flies. The devices utilized for the measurements are described elsewhere in this paper.

On two occasions, a Weston photographic light meter was used to
establish the difference, if any, in reflected light (or heat) from the colored and white areas of the dairy animal skins. The observation periods selected were clear days with slight breezes from the northwest. By holding the exposed surface of the light meter cell within 3 inches (7.5 cm.) and parallel to the animal surface, a reading in an arbitrary scale was obtained from the meter indicator which, later, was recalculated to foot candles.

4. Data

a. Temperature and Light Intensity

Thermocouple measurements of the temperatures within the mantle and on the surface of the host animal were observed usually to differ greatly from the macrotemperatures, and they fluctuated with changes of macrotemperature, macrohumidity and light intensity.

The depth of the mantle was determined by whether the flies rested on the hairs or on the skin. Another factor was the distance from the host's body at which the macrotemperature began to show a departure from the influence of the host animal body heat, a distance found to be approximately 0.5 inches (1.25 cm.) from the skin.

Within the mantle the air currents are minimized both by the friction of the animal hairs and by the general contours of the animal surface. With a minimum of air motion to dissipate body heat within the mantle, and a normal body temperature of about 100°F, it is obvious that any modification of the air temperature within the mantle (microtemperature) would be from an external source. Such a
change in the microtemperature would not necessarily occur throughout
the mantle, and therefore horn fly populations would move to the more
favorable microclimate.

Light intensity appeared to be a major controlling factor in the
distribution of horn flies on all the test animals. On clear, warm
days the flies were found on the dark-colored areas of bicoloored
cattle, especially on the sunlit surfaces, the white or light colored
areas apparently reflecting more light and heat (Fig. 14). The apparent
effect light had on the temperatures of the various skin areas examined
may be determined from data in Table 6. Notice the difference between
the macrotemperature (38°F) and the microtemperature within the man-
tle, where even on the shaded side of the animal the microtemperature
was above the minimum macrotemperature of 65°F preferred by the fly.
Jersey cows usually had fewer horn flies than did the bicoloored
Guernseys. The color of the Jerseys was usually a uniform grayish-
tan, a shade that appeared to absorb and reflect light equally.
Guernsey cattle, being tan and white, appeared to support the same
number of flies as did the Jersey cattle. According to Tables 7 and 8
there was little difference between the temperatures of colored skins
or mantles of Guernsey and Holstein cattle.

As the macrotemperature increased, so did the skin temperature
when clear or partly cloudy skies occurred. Under overcast skies the
temperature of the skin tended to remain cool, but would warm rapidly
when the sun broke through. The darker the skin, the more heat is
absorbed and less is reflected. Horn flies were observed on the
Figure 14. Horn fly preference to black surface on a clear, warm day.
Table 6. A comparison of mantle and skin temperatures and light intensity. The macrotemperature was 38°F. The numbers in parentheses are the horn fly counts relative to the temperature data, 1961.

<table>
<thead>
<tr>
<th>Location</th>
<th>Skin color</th>
<th>Sunlit</th>
<th>Shaded flank</th>
<th>Belly</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mantle (0.5&quot;)</td>
<td>Black</td>
<td>92(14)</td>
<td>95(7)</td>
<td>69(0)</td>
</tr>
<tr>
<td></td>
<td>White</td>
<td>92(11)</td>
<td>96(4)</td>
<td>69(0)</td>
</tr>
<tr>
<td>Skin</td>
<td>Black</td>
<td>105(14)</td>
<td>106(7)</td>
<td>96(0)</td>
</tr>
<tr>
<td></td>
<td>White</td>
<td>101(11)</td>
<td>101(4)</td>
<td>95(0)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Light intensity (fc)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black</td>
</tr>
<tr>
<td>White</td>
</tr>
</tbody>
</table>

** White belly only.
* Indicator needle passed maximum reading on meter.
Table 7. A comparison of skin temperatures of Holstein, Guernsey, and Jersey heifers at 3 selected macrotemperatures. The numbers in parentheses are the average horn fly counts relative to the temperature data, 1959 and 1960.

<table>
<thead>
<tr>
<th>Macro-temperature</th>
<th>Breed</th>
<th>Skin color</th>
<th>Sunlit flank</th>
<th>Shaded flank</th>
<th>Belly</th>
</tr>
</thead>
<tbody>
<tr>
<td>68°F</td>
<td>Holstein</td>
<td>Black</td>
<td>96(28)</td>
<td>95(37)</td>
<td>95(91)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>98(5)</td>
<td>95(0)</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Guernsey</td>
<td>Brown</td>
<td>93(6)</td>
<td>96(13)</td>
<td>97(49)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>93(0)</td>
<td>94(2)</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Jersey</td>
<td>Brown</td>
<td>97(7)</td>
<td>94(16)</td>
<td>93(27)</td>
</tr>
<tr>
<td>79°F</td>
<td>Holstein</td>
<td>Black</td>
<td>101(11)</td>
<td>101(14)</td>
<td>96(64)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>100(0)</td>
<td>100(0)</td>
<td>96(4)</td>
</tr>
<tr>
<td></td>
<td>Guernsey</td>
<td>Brown</td>
<td>103(0)</td>
<td>103(16)</td>
<td>94(48)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>103(0)</td>
<td>99(0)</td>
<td>95(0)</td>
</tr>
<tr>
<td></td>
<td>Jersey</td>
<td>Brown</td>
<td>102(0)</td>
<td>107(15)</td>
<td>100(18)</td>
</tr>
<tr>
<td>92°F</td>
<td>Holstein</td>
<td>Black</td>
<td>115(0)</td>
<td>109(0)</td>
<td>99(93)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>110(0)</td>
<td>107(0)</td>
<td>98(10)</td>
</tr>
<tr>
<td></td>
<td>Guernsey</td>
<td>Brown</td>
<td>113(0)</td>
<td>112(1)</td>
<td>103(46)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>110(0)</td>
<td>109(0)</td>
<td>101(16)</td>
</tr>
</tbody>
</table>

* No data available.
** White belly only.
Table 3. A comparison of air temperatures within the mantle of Holstein, Guernsey and Jersey heifers at 3 selected macrotemperatures. The numbers in parentheses are the average born fly counts relative to the temperature data, 1959 and 1960.

<table>
<thead>
<tr>
<th>Macrotemperature and sky condition</th>
<th>Breed</th>
<th>Skin color</th>
<th>Spine</th>
<th>Sunlit flank</th>
<th>Shaded flank</th>
<th>Belly</th>
</tr>
</thead>
<tbody>
<tr>
<td>71°F (Mod. cloudy)</td>
<td>Holstein</td>
<td>Black</td>
<td>71(16)</td>
<td>71(69)</td>
<td>71(114)</td>
<td>#</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>73(0)</td>
<td>72(0)</td>
<td>71(8)</td>
<td>74(4)</td>
</tr>
<tr>
<td></td>
<td>Guernsey</td>
<td>Brown</td>
<td>76(4)</td>
<td>74(18)</td>
<td>74(25)</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>78(0)</td>
<td>80(3)</td>
<td>73(12)</td>
<td>74(8)</td>
</tr>
<tr>
<td></td>
<td>Jersey</td>
<td>Brown</td>
<td>71(0)</td>
<td>73(34)</td>
<td>70(29)</td>
<td>74(0)</td>
</tr>
<tr>
<td>80°F (Clear)</td>
<td>Holstein</td>
<td>Black</td>
<td>104(2)</td>
<td>101(38)</td>
<td>97(131)</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>101(0)</td>
<td>106(0)</td>
<td>97(0)</td>
<td>97(32)</td>
</tr>
<tr>
<td></td>
<td>Guernsey</td>
<td>Brown</td>
<td>92(0)</td>
<td>92(1)</td>
<td>87(22)</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>100(0)</td>
<td>92(0)</td>
<td>87(0)</td>
<td>90(2)</td>
</tr>
<tr>
<td></td>
<td>Jersey</td>
<td>Brown</td>
<td>94(0)</td>
<td>91(4)</td>
<td>82(22)</td>
<td>90(5)</td>
</tr>
<tr>
<td>86°F (Cloudy)</td>
<td>Holstein</td>
<td>Black</td>
<td>91(0)</td>
<td>90(7)</td>
<td>91(90)</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>95(0)</td>
<td>91(0)</td>
<td>92(3)</td>
<td>86(35)</td>
</tr>
<tr>
<td></td>
<td>Guernsey</td>
<td>Brown</td>
<td>92(0)</td>
<td>94(10)</td>
<td>91(17)</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>White</td>
<td>94(0)</td>
<td>93(0)</td>
<td>91(2)</td>
<td>91(9)</td>
</tr>
<tr>
<td></td>
<td>Jersey</td>
<td>Brown</td>
<td>93(0)</td>
<td>89(15)</td>
<td>91(14)</td>
<td>91(7)</td>
</tr>
</tbody>
</table>

* White belly only.
white- or light-colored areas of cattle only when in the shade or when the sky was overcast and the day was cool. As the skin temperature surpassed the normal body temperature of the host, the flies moved to the more suitable areas on the shaded parts of the animals and especially around the navel and along the belly midline (Table 7). The microtemperature ranges in which horn fly populations were greatest was from approximately 90 to 95°F (32.5 to 35°C) for mantle temperatures and from approximately 95 to 100°F (35 to 38°C) for skin temperatures (Figs. 15 and 16).

b. Microhumidity

The relative humidity within the mantle, the microhumidity, as measured with a portable psychrometer fluctuates independently of the macrohumidity. During the 1960 horn fly season the relative microhumidity ranged from 47 to 75% for the herd of heifers (Tables 9, 10 and 11 and Fig. 17) while the relative macrohumidity of the biocenose ranged from 30 to 100% (Fig. 11). The relative microhumidity fluctuated independently of the relative macrohumidity and appeared to be influenced by the amount of radiant heat absorbed by the heifer.

5. Discussion

The difference between the macroclimate and the microclimate in biocenose of the horn fly is of great importance to the fly. Although the macroclimate determines the emergence of adults, their distribution
Figure 15. Relation of horn fly populations to average skin temperatures of three breeds of heifers, 1960.
Figure 16. Relation of horn fly populations to average air temperatures within the mantles of three breeds of heifers, 1960.
Table 9. Relative microhumidities of mantles of Holstein heifers observed during various relative macrohumidities. The numbers in parentheses are the horn fly counts relative to the relative macrohumidity data, 1960.

<table>
<thead>
<tr>
<th>Relative macrohumidity (%)</th>
<th>Hair color</th>
<th>Sunlit flank</th>
<th>Shaded flank</th>
<th>Belly</th>
</tr>
</thead>
<tbody>
<tr>
<td>48</td>
<td>Black</td>
<td>56(0)</td>
<td>62(4)</td>
<td>58(124)</td>
</tr>
<tr>
<td></td>
<td>White</td>
<td>58(0)</td>
<td>62(0)</td>
<td>50(6)</td>
</tr>
<tr>
<td>59</td>
<td>Black</td>
<td>64(0)</td>
<td>64(0)</td>
<td>62(134)</td>
</tr>
<tr>
<td></td>
<td>White</td>
<td>64(0)</td>
<td>68(0)</td>
<td>68(8)</td>
</tr>
<tr>
<td>62</td>
<td>Black</td>
<td>58(0)</td>
<td>49(128)</td>
<td>57(240)</td>
</tr>
<tr>
<td></td>
<td>White</td>
<td>54(0)</td>
<td>51(0)</td>
<td>57(38)</td>
</tr>
<tr>
<td>63</td>
<td>Black</td>
<td>62(43)</td>
<td>60(65)</td>
<td>60(87)</td>
</tr>
<tr>
<td></td>
<td>White</td>
<td>58(0)</td>
<td>64(0)</td>
<td>60(87)</td>
</tr>
<tr>
<td>66</td>
<td>Black</td>
<td>71(11)</td>
<td>72(14)</td>
<td>73(64)</td>
</tr>
<tr>
<td></td>
<td>White</td>
<td>72(0)</td>
<td>73(0)</td>
<td>74(4)</td>
</tr>
<tr>
<td>70</td>
<td>Black</td>
<td>62(4)</td>
<td>65(87)</td>
<td>65(94)</td>
</tr>
<tr>
<td></td>
<td>White</td>
<td>62(0)</td>
<td>63(0)</td>
<td>66(16)</td>
</tr>
<tr>
<td>75</td>
<td>Black</td>
<td>61(32)</td>
<td>64(98)</td>
<td>67(11)</td>
</tr>
<tr>
<td></td>
<td>White</td>
<td>67(0)</td>
<td>65(0)</td>
<td>67(11)</td>
</tr>
</tbody>
</table>
| Relative macromeridities of mantles of Chamaemy mollusks observed during various
| relative to the relatives. The numbers in parentheses are the
| Relative
<table>
<thead>
<tr>
<th>macromeridities (%)</th>
<th>Hair color</th>
<th>Shaded flank</th>
<th>Spine flank</th>
<th>Belly</th>
</tr>
</thead>
<tbody>
<tr>
<td>48</td>
<td>Brown White</td>
<td>55(0) 60(0)</td>
<td>47(0) 55(0)</td>
<td>62(0)</td>
</tr>
<tr>
<td>62</td>
<td>Brown White</td>
<td>57(4) 60(4)</td>
<td>62(21) 61(0)</td>
<td>56(18)</td>
</tr>
<tr>
<td>63</td>
<td>Brown White</td>
<td>58(7) 60(7)</td>
<td>62(21) 61(0)</td>
<td>56(18)</td>
</tr>
<tr>
<td>67</td>
<td>Brown White</td>
<td>59(1) 60(1)</td>
<td>62(4) 60(4)</td>
<td>56(18)</td>
</tr>
<tr>
<td>70</td>
<td>Brown White</td>
<td>60(21) 60(21)</td>
<td>62(21) 60(21)</td>
<td>56(18)</td>
</tr>
<tr>
<td>75</td>
<td>Brown White</td>
<td>62(3) 63(3)</td>
<td>63(12) 64(12)</td>
<td>59(12)</td>
</tr>
<tr>
<td>78</td>
<td>Brown White</td>
<td>72(1) 72(1)</td>
<td>72(21) 72(21)</td>
<td>72(21)</td>
</tr>
</tbody>
</table>
Table II. Relative microcohumsities of mantles of Jersey heifers observed during various relative microcohumsity. The numbers in parentheses are the born fly counts relative to the relative microcohumsity data, 1950.

<table>
<thead>
<tr>
<th>Relative microcohumsity (%)</th>
<th>Spine</th>
<th>Shield flank</th>
<th>Belly</th>
</tr>
</thead>
<tbody>
<tr>
<td>48</td>
<td>50(8)</td>
<td>57(34)</td>
<td>51(34)</td>
</tr>
<tr>
<td>59</td>
<td>64(0)</td>
<td>61(36)</td>
<td>61(36)</td>
</tr>
<tr>
<td>62</td>
<td>64(1)</td>
<td>60(34)</td>
<td>60(34)</td>
</tr>
<tr>
<td>63</td>
<td>64(7)</td>
<td>69(22)</td>
<td>69(22)</td>
</tr>
<tr>
<td>64</td>
<td>68(5)</td>
<td>73(11)</td>
<td>72(13)</td>
</tr>
<tr>
<td>65</td>
<td>74(0)</td>
<td>64(22)</td>
<td>64(22)</td>
</tr>
<tr>
<td>66</td>
<td>67(7)</td>
<td>69(12)</td>
<td>69(12)</td>
</tr>
<tr>
<td>67</td>
<td>68(24)</td>
<td>66(4)</td>
<td>66(4)</td>
</tr>
<tr>
<td>70</td>
<td>70(57)</td>
<td>70(9)</td>
<td>70(9)</td>
</tr>
</tbody>
</table>
Figure 17. Relation of horn fly populations to average relative microhumidities of the three breeds of heifers, 1960.
on the host animals, and the virtual end of the horn fly season, the microclimate within the mantle about the host animal appears to determine the ability of the fly to withstand extreme variations in the macroclimate. The temperature and relative humidity within the mantle appear to be dependent upon the skin temperature of the host and the ability of the hairs of the skin to help retain atmospheric moisture within the mantle.

The thermocouple measurements of heifer skin temperatures recorded during this study corroborate the data obtained by Matthyssee (1946). The darker the skin, the more heat is absorbed and the warmer the skin, the better the horn flies like it up to a point, beyond which the flies seek more suitable locations. On very warm days, when the macrotemperature is above 90°F and the sky is clear, the skin temperature of a Holstein will vary from approximately 115°F on a black spot of the back to 96°F on a black spot on the shaded side or on the white of the belly. During such conditions less than 10% of the flies observed on one animal were on the sunny area. On Jersey animals under the same conditions, over 90% of the flies were observed on the shaded parts.

Regarding the occurrence of horn flies on the white skin in sunlight, the flies have been observed on such areas only during the early morning hours while the macrotemperature is still cool. It is believed by the author that, during the warmer hours of a day, the reflected sunlight is intensified by the white areas and tends to blind the flies more than does that reflected from the colored areas. The flies are
commonly found on the white skin of the belly, especially about the navel and between the udder and the hind legs during hot weather (Fig. 18).

A review of the micro-environmental data indicated the following optimum micro-environmental factors for horn flies:

1. Temperature of 95 to 100°F at the skin surface (Fig. 15)
2. Temperature of 85 to 95°F (mean of 90°F) within the mantle (Fig. 16)
3. Relative humidity of 55 to 65% (mean of 60%) within the mantle (Fig. 17).

The relative microhumidity and macrohumidity which were recorded during seasonal peaks of horn fly populations were approximately the same, 60% and 65%, respectively.

The optimum micro-environmental conditions observed during the warmer days of the two horn fly seasons (macrotemperature above 75°F) were most commonly observed along the belly midline and the shaded flank. When such conditions existed there, the majority of the flies on each animal were found there (Tables 6 through 11).

According to this study, wind was a factor in the location of fly populations on the host animals only when the macrotemperature was either below 52°F or above 86°F and wind velocity was greater than 20 miles per hour. When the temperatures were within that range, wind of such velocity did not appear to modify the microenvironment.

The micro-environment protects the flies from adverse macrocli-
Figure 18. Horn flies on white skin between the udder and hind leg of a Guernsey heifer during warm weather.
mathical conditions. Two examples are: 1) the hair of the cow acts as a windbreak for the flies and protects them from being washed away during heavy rains; 2) during periods of low relative macrohumidity, the more optimum microhumidity prevents the flies from desiccating. During the last month of the horn fly season, when the macrotemperature decreases below 40°F, most of the flies that die apparently are those that have been brushed off the host and become chilled to the extent that they are unable to fly back to the host. Those flies which remain on the host during cold spells and do not leave the host for any reason, may survive for several days within the mantle. The skin temperatures of several Holstein heifers were recorded during such conditions and found to be above 85°F and the mantle temperature was between 80° and 85°F.

As a final example of the importance of the mantle about the host, when the temperature and relative humidity were measured 0.25 inches (6.25 mm.) from the skin of a Jersey heifer on a cool fall day the readings were 87°F and 65% respectively, whereas 1.0 inch (25 mm.) from the skin in the same area the temperature was 53°F and the relative humidity was 40%.
V. CONCLUSIONS

A noticeable increase in the horn fly population occurs within two days after the weather stabilizes near the optimum for horn flies. The largest horn fly populations occur during periods when the minimum macrotemperatures are above 65°F. Minimum daily macrotemperature depressions below 55°F tend to retard horn fly populations. The optimum macroclimate for the horn fly is 73 to 80°F macrotemperature, 65 to 90% relative macrohumidity, scattered light showers, and no wind.

Low macrotemperatures (below 40 to 45°F) have a retarding effect on the emergence of adult flies and cause a decrease in the adult population due to the flies leaving the host to oviposit and on becoming chilled and inactive are unable to return to the host. Horn flies can withstand macrotemperatures (above 90°F) when the relative macrohumidity is above 40%, but by remaining within the mantle of relative microhumidity about the host they can withstand a relative macrohumidity below 40%.

Horn flies prefer dark colored animals or dark skin to light or white due to the reflective characteristics of the different skin and hair colors. Dark skin and hair absorb more heat than does white or light skin and hair.

When the microclimate of the sunlit areas of the host are unsuitable, the horn flies seek more suitable conditions elsewhere on the same animal, usually the shaded side or the belly midline. The
preferred micro-environment for horn flies includes a skin temperature of 95 to 100°F, a mantle air temperature of 85 to 95°F, a relative microhumidity of 55 to 65%, and a black surface.

It is clear from these experiments that as the biotopes differ so does the distribution of horn fly populations for each biotope. Any modification in the macroclimate causes a change in the spatial distribution of horn flies within each biotope.
VI. SUMMARY

A preliminary experiment was conducted during the horn fly season at Blacksburg, Virginia from May through September, 1959, to determine the relationship of weather conditions to horn fly populations on 3 breeds of dairy heifers. Daily records of the fly populations on 10 animals selected at random from a mixed herd of Holstein, Guernsey, and Jersey yearling heifers were made. In addition, the daily minimum and maximum macrotemperatures and relative humidities, the approximate wind direction, and the amount of sunlight or cloud coverage were recorded.

Usually there was a significant difference between the number of horn flies on Holstein and that on Guernsey and Jersey heifers. Horn flies generally preferred the dark colored areas of bicolored cattle during the hours of daylight, and they preferred the black of the Holstein rather than the tan of the Guernsey. When the macrotemperature was above 85°F, many of the flies were found on the white skin of the belly and udder area of a heifer. During inclement weather the flies were observed on both the white and dark colored areas of all the heifers. Macrotemperature and relative humidity influenced the horn fly populations within the biocenose. Light rain and winds of less than 20 miles per hour were found to have a negligible effect on the number of flies in the populations; however, significant population decreases were attributed to heavy rain, wind in excess of 20 miles per hour. Often, when the macrotemperature was
below 55°F, light rain or wind of low velocity influenced movement of
the flies to more sheltered areas on the host. The apparently pre-
ferred macroclimate for horn flies was: temperature of 73 to 80°F;
relative macrohumidity of 65 to 90%; scattered light showers; and no
wind.

During the horn fly season of 1960, a second experiment was
conducted to correlate the effect of the macro-environment on the
micro-environment within the ½ inch mantle of the animal, and also
to correlate the locations of horn flies within this mantle with
various factors of the micro-environment. (Daily macro-environmental
data, including air temperature, relative humidity, wind direction and
velocity, amount of cloud coverage, and precipitation, were recorded
as in the preliminary experiment of 1959.) Methods for measuring the
micro-environment were devised, and the data obtained were analysed
statistically and interpreted. Accordingly, the effects on horn fly
populations of dark skin color, low temperature, and low humidity
were highly significant at the 1% level; the effects on horn fly
populations of high humidity and precipitation were significant at
the 5% level; and the effect of high temperature on horn flies was
not significant at the 5% level.

According to the results of the second experiment, the horn
flies apparently sought certain micro-environmental conditions which
were most commonly observed on Holstein heifers. Within the mantle
of micro-environment, horn flies appeared to prefer an air temperature
of about 85°F, a skin temperature of about 97°F, and a relative
humidity of about 65%. When such conditions were not available to the horn flies on the sides and backs of Holstein heifers, the flies usually found near optimum conditions along the belly midline for each of the 3 breeds of heifers.
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IX. VITA

Neal Oliver Morgan was born May 13, 1928, at Los Angeles, California, the son of Homer K. and Helen B. Morgan. He graduated from Brown Military Academy, San Diego, California in September 1945 and attended the University of Southern California from 1945 until 1947. He served in the Artillery branch of the U. S. Army from 1949 to 1953 during which time he married the former Mary J. Holmen, in December 1952, and they are the parents of two children - Helen Marie, born October 6, 1953, and Richard Homer, born July 4, 1955. Mr. Morgan attended South Dakota State College from 1954 until 1957 receiving a B.S. degree in 1956 and a M.S. degree in 1957. He was a research assistant in entomology with the Virginia Agricultural Experiment Station while studying at Virginia Polytechnic Institute, 1958-1961. He received the Ph.D. degree with a major in entomology from the Virginia Polytechnic Institute in 1962 and is a member of the Entomological Society of America, American Association for the Advancement of Science, American Institute of Biological Sciences, and the Society of the Sigma Xi.

Neal Morgan
THE AUTOECOLOGY OF THE ADULT HORN FLY, *HAEMATOBIA IRRITANS* (L.),
(DIPTERA: MUSCIDAE) ON DAIRY CATTLE

by

Neal Oliver Morgan

Abstract

A preliminary experiment was conducted during the horn fly season at Blacksburg, Virginia from May through September, 1959, to determine the relationship of weather conditions to horn fly populations on 3 breeds of dairy heifers. Daily records of the fly populations on 10 animals selected at random from a mixed herd of Holstein, Guernsey, and Jersey yearling heifers were made. In addition, the daily minimum and maximum macrotemperatures and relative humidities, the approximate wind direction, and the amount of sunlight or cloud coverage were recorded.

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During the horn fly season of 1960, a second experiment was conducted to correlate the effect of the macro-environment on the micro-environment within the ½ inch mantle of the animal, and also to correlate the locations of horn flies within this mantle with various factors of the micro-environment. (Daily macro-environmental data, including air temperature, relative humidity, wind direction and velocity, amount of cloud coverage, and precipitation, were recorded as in the preliminary experiment of 1959.) Methods for measuring the micro-environment were devised, and the data obtained were analysed statistically and interpreted. Accordingly, the effects on horn fly populations of dark skin color, low temperature, and low humidity were highly significant at the 1% level; the effects on horn fly populations of high humidity and precipitation were significant at the 5% level; and the effect of high temperature on horn flies was not significant at the 5% level.

According to the results of the second experiment, the horn
flies apparently sought certain micro-environmental conditions which were most commonly observed on Holstein heifers. Within the mantle of micro-environment, horn flies appeared to prefer an air temperature of about 85°F, a skin temperature of about 97°F, and a relative humidity of about 65%. When such conditions were not available to the horn flies on the sides and backs of Holstein heifers, the flies usually found near optimum conditions along the belly midline for each of the 3 breeds of heifers.