1973

Mating Behavior of the European Corn Borer, Ostrinia nubilalis (Hubner)

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MATING BEHAVIOR OF THE EUROPEAN CORN BORER, *OSTRINIA NUBILALIS* (HÜBNER)

BY

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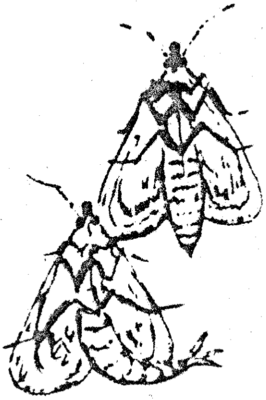
STATE UNIVERSITY OF NEW YORK

COLLEGE AT BROCKPORT

1973

Mating



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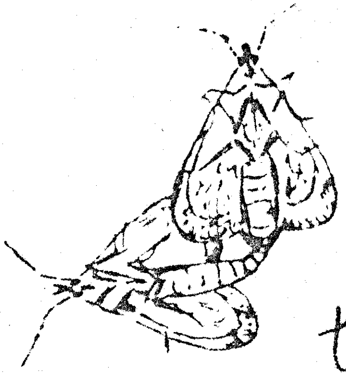

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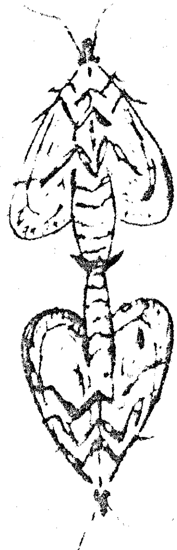

corn borer

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MATING BEHAVIOR OF THE EUROPEAN CORN BORER, *OSTRINIA NUBILALIS* (HÜBNER)

BY

HUGH L. RATIGAN

Under the supervision of Professor

ELMER J. CLOUTIER

ABSTRACT

The European corn borers for this study were raised on artificial diet. The adult moths were placed in a cage for mating and their behavior was observed. The moths' day-night cycle was reversed so that work with cinematography could be done in a darkened room during the day. Mating crosses were made between male and female adult moths from Minnesota, New York, and Wisconsin strains. The moths' mating behavior is described and the crossing of geographical strains is documented.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to my advisors Dr. J. Mosher and Dr. D. Smith for their aid and encouragement with the behavioral and physiological aspects of my research.

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I

INTRODUCTION

The European corn borer has been a problem in the United States since its introduction sometime during the early part of the twentieth century. It is thought that it may have been imported from Hungary or Italy in broom-corn. This corn borer belongs to the family Pyralidae and has an adult body length of less than 1.5 centimeters. It has become a major agricultural pest of large corn growing areas both in the United States and in Canada. Corn borer attack tends to result in poor ear development, broken stalks, and dropped ears which reduces yield and increases expense of harvesting.

The purpose of this study was to observe and document the mating behavior of the European corn borer, *Ostrinia nubilalis*. Work has been done in determining the sex pheromone, proper diet, acoustic sensitivity, morphology, spermatogenesis, and neuroendocrine complex of the European corn borer but little work has been reported on the use of cinematography for filming the mating behavior of the moth. A major article used for reference with cinematography was the work done by Sparks and Facto (1966). Observations of mating behavior of the European corn borer by Klun (1961), Loughner (1971), and Pesho

(1961) were most helpful in this study.

The objects of this communication are, first, to better describe the mating behavior of the European corn borer moth through the use of cinematography and, second, to determine if moths of different geographical strains will mate. It is hoped the former may reveal some hitherto unnoticed activity which could suggest a method of interfering with reproductive success. The latter was a test of the hypothesis that reproductive isolation may have developed as a consequence of geographical distribution.

II

LITERATURE REVIEW

Many field study reports were made on the European corn borer in the early 1900's after its probable introduction in broomcorn (Smith, 1920). Vinal and Caffrey reported the presence of the corn borer in Massachusetts in 1919 and suggested methods of control. During the years 1922-1923 Crawford and Spencer studied the European corn borer in Ontario. Investigations of the corn borer were reported by Caffrey and Worthley in 1927. Also during this year O'Kane and Lowry reported a study on the life history of the European corn borer in New Hampshire from 1923-1926.

In 1931, Bottger and Kent investigated this insect in Michigan. Ficht (1936) reported on the corn borer in Indiana. The European corn borer was reported to be present on the Eastern Shore of Virginia by Jones, Walker, and Anderson in 1939. Numerous articles on the European corn borer have appeared since. It has migrated westward since the 1930's infesting areas that are large producers of corn. The problems with this insect pest have become so great that the Federal Government established a laboratory in Ankeny, Iowa, to coordinate research for control of the European corn borer. Research on this corn borer's behavior will aid in its control.

During the early part of the twentieth century, reports of observations made on the senses of Lepidopterans began to appear. Forbes (1923) wrote about the tympanum of certain Lepidoptera and Eltringham (1933) worked with the senses of insects. Detail of the ommatidia in light and dark adapted conditions was given by Day (1941). Sight may play an important role in the recognition of a sex partner in the European corn borer. The studies on insect senses served as a foundation for insect behavioral research.

An early worker on the behavior of insects, (Richards, 1927), mentions that in some insects, feeding may play a particular role in inducing female receptiveness. The male cockroach secretes a liquid which incites the female to climb on his back enabling him to mate with her. Dickens (1936) worked with the scent glands of certain Phycitidae. He wrote about the diffusion of the gland secretions and dispersal of the scent promoted by the extension of the abdomen. This work is important since chemical attractants play a major role in mating behavior.

Snodgrass (1935) considers the structure of the reproductive organs in his text. An overall review of insect reproduction and reproductive systems is given by Davey (1965). The terminology applied to the reproductive systems in the European corn borer in this communication is that used by Drecktrah and Brindley (1967).

It was found by Sparks and Facto (1966) that the mating activity of the European corn borer moths occurs between the hours of 10 P.M. and 5 A.M., almost exclusively. The techniques used by Sparks and Facto were as follows: The moths to be photographed were kept isolated in 2 oz. plastic cups and upon emergence held separately until 9-10 P.M. The moths were chilled in a 40°F walk-in cooler before being transferred to the mating cage which was 10x12x4 inches. A Cine-Kodak camera was used with Kodak 16 mm High Speed Infrared using an aperature of f/2 and the exposure duration was about 1/10 second for each frame of exposed film. The camera was mechanized to take one picture every 12 seconds. Very little detail of mating performance of the corn borer could be established. They were able to obtain information on feeding behavior, flight activity, mating habits, and to document the existence of a sex attractant. This was the only reference found relating to photographic work with the European corn borer.

Fatzinger and Asher (1971) described the mating behavior of Dioryctria abietella, (Lepidoptera) with the nocturnal "calling" behavior of the females at the time of sex-pheromone release. This was observed under light-dark cycles of 12 hours light and 12 hours darkness. Calling of the female began between 5-6 hours after dark and was maximum after 9 hours of darkness, ceasing just prior to the onset of the light phase. Matings occurred only during periods of female calling. The female calling behavior is a dorsal bending of the abdomen so that it projects between the female's wings. When the resting males were confronted with the calling females, they became excited and began crawling about with their abdomens curved ventrally fluttering their wings in short bursts of ca. 0.25 seconds and waving their antennae at a frequency of ca. 4.5 beats/second. Upward curvature of the female's abdomen and extension of the ovipositor were maintained through-out most of pre-copulatory behavior. This upward curvature of the female's abdomen appeared to promote clasping by placing her genitalia in line with the male's claspers. The extension of the ovipositor also appeared to facilitate mating by exposing the ostium bursa through which the aedeagus of the male is inserted for copulation.

The research done by Dustan (1964) with the Oriental Fruit Moth states that females ready to mate attracted the males and induced a mating response in them that was characterized by continuous vibration of the wings, a curving downward and forwards of the abdomen, and short, darting runs or flights. Several attempts by one or more males were usually required before the aedeagus was inserted in the female. Once this occurred, the mated moths seldom moved until mating was finished. The male's attraction to the females appeared to end once the two were coupled. On a few occassions when near couples were attempting to mate, males became so excited that they locked their own genitalia firmly together and remained attached for several hours. All couplings of females and males were not successful. Most moths mated between mid-afternoon and an hour after sunset. Multiple matings in the Oriental Fruit Moth were recorded.

Callahan (1958a) describes the behavior of the corn earworm imago at emergence. He states that pupae became active and rotate. Abdominal movements are seen and the pupal case splits open along the median dorsal line of the thorax with the imago finally working itself free. Copulation was never observed on the first complete night after emergence nor on emergence night. Mating activity started on the second complete night after emergence. All copulations were observed to occur after 1 A.M. and last from 1 hour to 1 hour and 45 minutes. After copulation, the moths flew to a corner moving their wings up and down two or three times. They than settled down in a resting position for the remainder of the night.

In the Spruce Budworm Moths, Outram (1971) states that the males mated only once within a 24 hour period. They were most responsive when 2 to 4 days old and least responsive immediately after emergence (less than 0.5 day old). The females mated most readily when less than 0.5 day old and became progressively less attractive or less receptive with age. Mated females were not as attractive as unmated females. Mating was highest when 2 to 4 day old males were paired with females less than 0.5 day old.

Pesho (1961) states that the presence or absence of a spermatophore is conclusive evidence of whether or not a mating occurred in the European corn borer female. In some instances he found more than one spermatophore in a female indicating that multiple matings can and do occur. Data collected from spermatophore counts of feral populations gave a range of 65% to 100% females mated and 8% to 43% multiple matings.

Drecktrah and Brindley (1967) point out in their work that multiple matings occur between the male and female European corn borer moths. When a pair of moths is caged one day, one mating occurs. If the pair is caged two days, two matings occur. If the pair is caged three days, three matings occur. In one case one female mated four times.

In a study done by Loughner (1971) it is mentioned that female multiple matings were few but did occur in the European corn borer. Males will mate with virgin females every day. Neither the male or female will mate more than once in a 24 hour period. The female for the most part plays a passive role in mating. Loughner feels that as temperatures fall with reduced light, the female releases a chemical attractant. She is sometimes seen moving her wings actively perhaps dispersing the chemical attractant in the air. A pumping of her abdomen was also noted after the wing activity. Biotic factors such as mating age, age preference for a mate, and crowding had no effect on mating behavior.

Fatzinger and Asher (1971) observed multiple matings with both male and female <u>Dioryctria abietella</u>.

Loughner and Brindley (1971) found that there is a linear relationship between temperature drop and mating frequency within a temperature range of 30°C to 21.2°C.

At light intensities below 100 foot candles (ft.-c.), cycling temperatures affect mating more than does light. In a frequency distribution they showed that most mating occurred between the fourth and sixth hour after sunset. The temperatures at which the highest frequency for mating occurred was 20.6°C. Moonlight did seem to have an effect on the mating of the adult moths. Only when the full moon went behind clouds did the moths in the experimental cage mate. As soon as the full moon appeared from behind the clouds attempts to initiate mating stopped. It was not known if direct moonlight affected the male or female or inhibited both. It was found that a wind speed of 10.3 mph during scotophase completely inhibited mating but a 3 mph wind did not stop mating.

It was stated by Daterman (1968) that the European pine shoot moth became active and moved when the light intensity was decreased to 10 ft.-c. Females became more active particularly below the 5 ft.-c. level. Stimulated males exhibited precopulatory movements which included rapid wing fluttering, anteriorly curved abdomens, and opening and closing of the genital valvae. The males continued rapid wing fluttering and moved rapidly in a circular fashion in obvious attempts to locate the female. Once the female was located, there was no further courtship activity and copulation occurred immediately. In this moth, it was confirmed that females mate only once if a normal spermatophore is received from the male. Females once fertilized are never again attractive to a male.

Klun and Brindley (1970) determined that the male European corn borer is stimulated by cis-11-tetradecenyl acetate (cis-11-tda). This sex attractant has also been identified as the natural sex stimulant of the red-banded leaf roller, Argyotaenia velutinana (Walker).

Klun (1968) found that the sex pheromone is a strong electron captor, is nonsaponifiable, is soluble in polar organic solvents, and is highly stable at standard conditions. He found that the males responded to the pheromone by taking part in a pre-copulatory "dance" with wings extended up and vibrating, genitalia extended, followed by an opening and closing clasper response. The excited state lasted as long as 5 minutes after the males had been exposed to the pheromone. The pheromone, kept in the laboratory at room conditions, kept its potency for more than 1 year. Once the male was stimulated, he oriented himself toward the source of the vapor. The male responded better when the laboratory temperature was maintained at 20-30^{o}C. The antennae of the male are involved in the sex pheromone response and removal of the antennae resulted in the male's inability to respond to the pheromone. The ninth and tenth segments of the female contain the accessory gland and reservoir for the active substance.

Klun and Robinson (1971) found that the flight orientation of the European corn borer males to the location of the females or to cis-11-tda is inhibited by the presence of trans-11-tda and 11-tetradecynl acetate (11-tdya). Thus, it was felt that such chemical inhibitors if released in the field would inhibit the mate-seeking ability of the European corn borer male and reduce the population of the pest in corn areas. They also found that although trans-11-tda and 11-tdya did inhibit flight orientation of the male corn borer, it did not inhibit precopulatory behavior.

Shorey (1964) mentions that the chemical released by Trichophusia ni female, plus moving air, stimulates and releases a complex sequence of male responses, one being arousal of the male from resting. He also found that the antennae were the principle site for the determination of the direction of odor source. In research on the Oriental Fruit Moth, George (1965) mentions that the pheromone caused the males to raise their antennae and whirl with fanning wings. If the antennae were cut off, they did not respond to the pheromone. If half of the antennae was present, then the mating reaction was nearly normal.

Traynier (1968) found that if a male Mediterranean Flour Moth detected sufficient concentration of sex pheromone in moving air, they appeared to be stimulated by waving one antennae alternately, walking at random with waving antennae and wing vibration while walking aimlessly or upwind. In still air, the male approached the female from below suggesting that a column of air beneath the female was charged with pheromone. He notes that the females normally emitted attractant from the upper walls or roof of their containers. This position might ensure that an optimum volume of air contains the attractant.

In a study done with the Eastern Spruce Budworm, Sanders (1969) confirms the location of the sex pheromone gland between the eighth and ninth segments of the moth. Receptive males respond to the pheromone by twirling around on the screen near the source of the attractant with the wings raised, frequently giving short bursts of rapid wingbeats. This is associated with opening and closing of the claspers and with attempts at copulation, which may be directed towards other males if the extruding female is inaccessible.

Sparks, Brindley, and Penny (1966) looked for genetic differences in 3 biotypes. Crosses were made between moths from Minnesota, Iowa, and Missouri indicating that diapause was genetically controlled. From the data collected it is indicated that the inheritance mechanism of this attribute is controlled by something other than a single pair of genes and is probably controlled by a multigenetic makeup which responds to temperature and photoperiod. Sensitivity to day-length could be a factor since Mutchmor (1959) mentions that there appears to be an excellent association between day-length in the latter part of July and the change in the incidence of diapause.

It was found by Chaudhury and Raun (1966) that germ cell maturation even went on in the pupal stage. Nearly 50% of the cysts in the 7 day old pupae contained sperm and the testes of a 1 day old adult held primarily mature sperm. When the moth reaches adulthood, it already contains its full complement of sperm. Loughner (1971) found that European corn borer males would successfully mate 1-6 hours, 24-30 hours, and 48-54 hours after emergence of the imago.

The following literature deals with some of the external factors which may influence the European corn borer in the field. Results by Hudon and LeRoux (1961) indicated that for all samplings of immature stages of Ostrinia nubilalis, differences between upper and lower halves of the stalks were with one exception consistently significant, i.e. density totals for all age intervals were consistently higher in the lower halves of the plants. It was found by Barlow (1963) that the number of European corn borer females in the first flight, and rainfall during the first flight, may be factors determining fluctuations in the numbers of Ostrinia nubilalis in the environment. Kira, Guthrie, and Huggans (1969) found that the availability of drinking water effectively increased the number of eggs produced and the resultant hatching of the European corn borer eggs. In the laboratory they found that a wet cotton pad on the screen cage assured the best results for egg masses and hatchability.

Moths have acoustic organs and sound may play a role in mating. Agee (1969) experimented with sound vibration in an attempt to determine whether the moths could be attracted to a sound source. He found that the European corn borer moths were particularly sensitive to sound at 25-kHz pulses and less sensitive at 60-kHz pulses. At a pulse train of 25-kHz the behavioral action was a quick fluttering of the wings.

Callahan (1965c) states that a red 7-w bulb burning in the cage caused the eyes of the corn earworm moths to glow and reflect light at night but not during the day. He feels that the night-adapted eyes of the moths are ideally suited for detecting point sources of infrared radiation, such as might be radiated by another moth. The fact that moths fly and mate in complete darkness would suggest that this is true. They might see their mates as IR patterns against a darker background.

Callahan also mentions many of his theories on insect communication. He has done much work with the corn earworm and has postulated that there must be more than one signal involved in the complex pattern of moth behavior that leads to mating. Scent itself is an electromagnetic transmitter and the moth antennae either detect, or couple to, the electromagnetic energy from the free floating scent molecules. He feels that the antennae are "tuned" to the various infrared and microwave frequencies of both scent molecules and the total IR emission of mates, and perhaps of host plants, too.

III
METHODS AND MATERIALS

The principal organism used in this research project was the adult European corn borer moth, Ostrinia nubilalis.

The corn borers were reared in the laboratory. Adults in wire and cheesecloth mating chambers oviposited eggs on wax paper. The eggs were collected and placed in the dark in incubators at 30°C. The larvae upon hatching were transferred to 1 oz. clear plastic cups containing sufficient diet for the development of the larvae. The wheat germ diet used was described by Beck, et. al. (1968). The larvae were reared in an incubator at 30°C. Pupation occurred usually between 12 and 17 days after the larvae hatched. The pupae were then collected and separated after their sex had been determined.

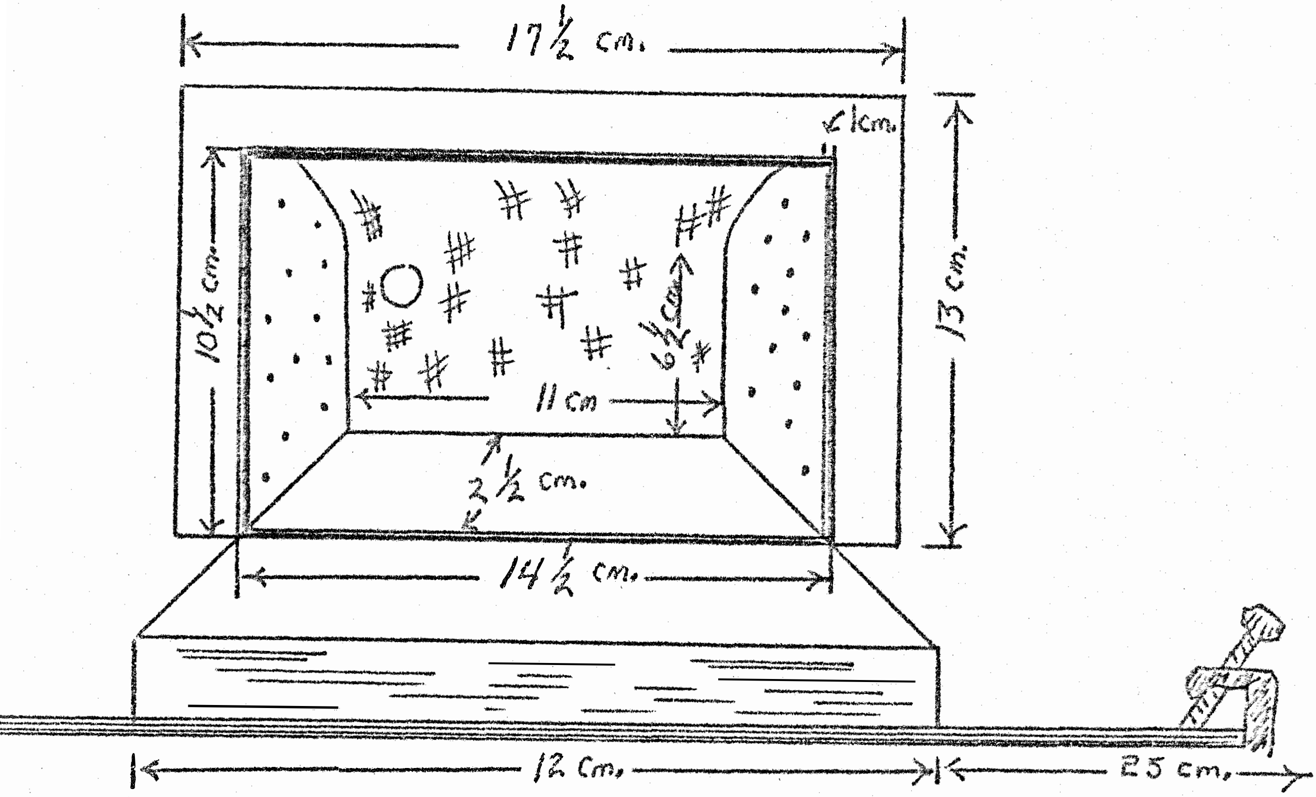
Once the moths had emerged from their pupal cases, they were placed in cages for observation of their behavior. Several different cages were used for observing the moths. One cage was made using balsa wood as a frame covered with clear plastic. Another type of cage was made using ¼ inch wire mesh covered with cheesecloth and/or clear plastic with glass petri dishes for the top and bottom. Plastic bags were also tried using a wire frame to support the plastic. One oz. plastic cups were used with only one pair of moths placed in each cup.

By placing moistened cotton, paper, or cheesecloth in the bottom of the cages, a relative humidity of between 75 and 80% was maintained.

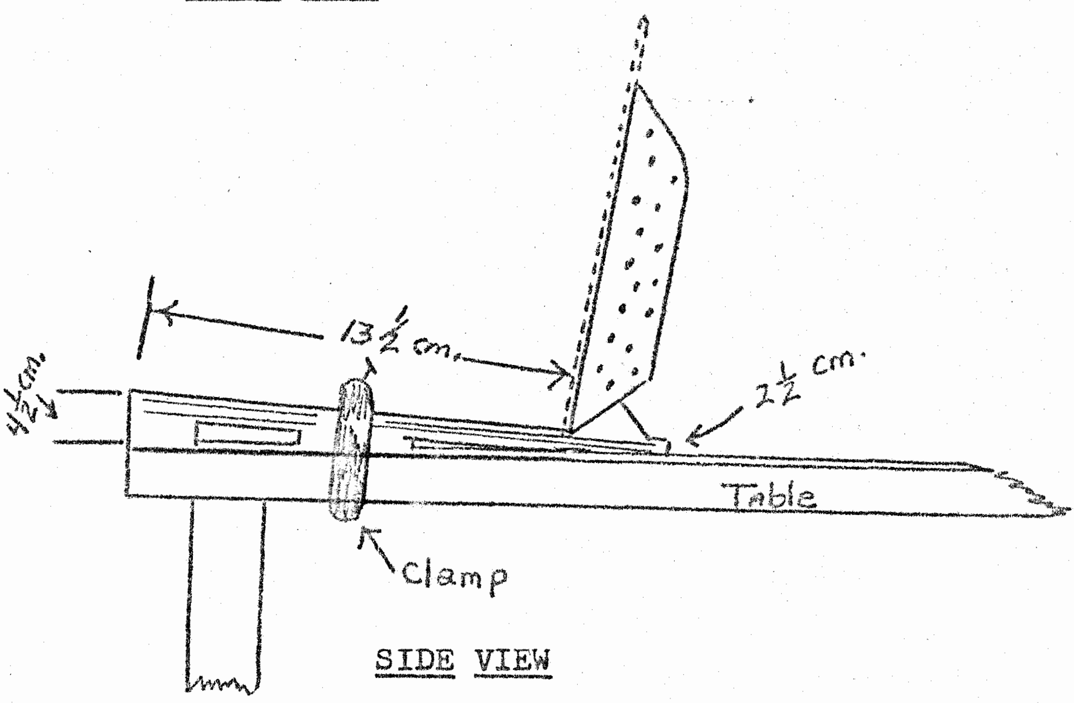
Preliminary observations were made between the hours of 10 P.M. and 5 A.M. on an hourly basis. Slide photographs were taken using fast black and white 35 mm film in a Miranda Sensorex Camera with a close-up lens attachment. A 7-w red bulb was used to illuminate the cage. This lighting had no effect upon the moth's behavior. It was from this type of lighting that the idea came to discontinue using the hot infrared illumination and instead use two 25-w red bulbs for filming the behavior of the moths.

The photographic cage, Figure A, was used for the cinematography work. To keep the humidity high in the cage cheesecloth was moistened and placed over the back of the cage. During the research project temperatures of 23°C during the day and about 18°C at night were kept, except when filming.

The moth's life span in the laboratory was ten to twelve days on the average. During this time, the adults were given only water as a means of sustenance. Kira, Guthrie, and Huggans (1969) found that water was most



FRONT VIEW



SIDE VIEW

Dimensions of the phtographic cage

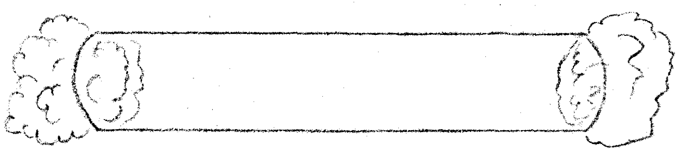
FIGURE A

essential for the production of viable eggs by the European corn borer.

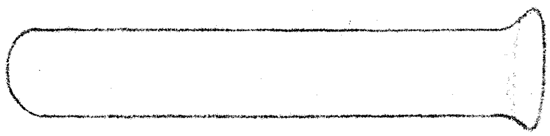
The moths were isolated in 1 oz. plastic cups and were exposed to simultaneous cycles of temperature and light. Their day-night cycle was reversed so that the moths were in the dark and cinematography work could be done during the daytime rather than during the 10 P.M. to 5 A.M. hours when the moths are found to mate. The photoperiod used was 14 hours of darkness (8 A.M. - 10 P.M.) and ten hours of light (10 P.M. - 8 A.M.). After the imagos had emerged, they were kept on this cycle until taken to the cinematography lab for observing and photographing.

Transferring the moths from the plastic cups was simplified by placing the moths in a refrigerator at 6°C for 5 to 10 minutes to reduce their metabolic rate. The moths crawled from the cups into a hollow glass tube plugged at one end with cotton. Once all the males were in one glass tube the open end was plugged also. The same procedure was followed with the female moths. The moths were taken to the cinematography studio and transferred into the cage for filming (Figure B).

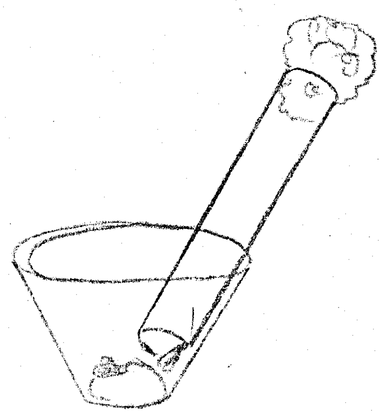
The following procedure was followed each time a new group of moths was transferred to the observation cage in



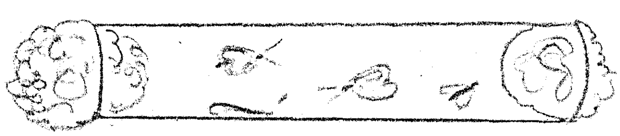
HOLLOW GLASS TUBE WITH COTTON PLUGS



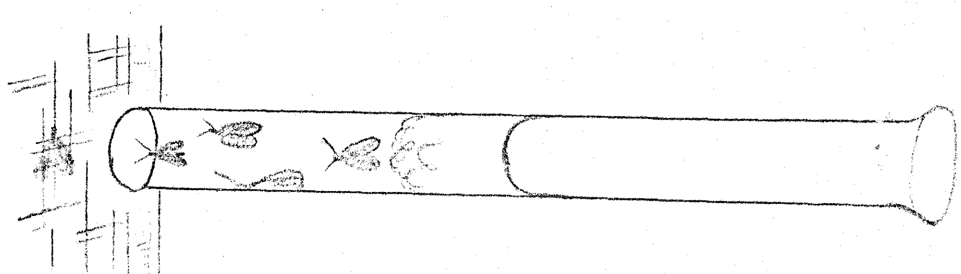
PLUNGER



MOTHS CRAWL INTO GLASS TUBE FROM
PLASTIC 1 oz. CUP



MOTHS NOW READY TO TRANSFER TO CAGE



MOTHS INJECTED INTO CAGE

PROCEDURE FOR MOTHS' TRANSFER INTO THE CAGE FOR PHOTOGRAPHING.

FIGURE B

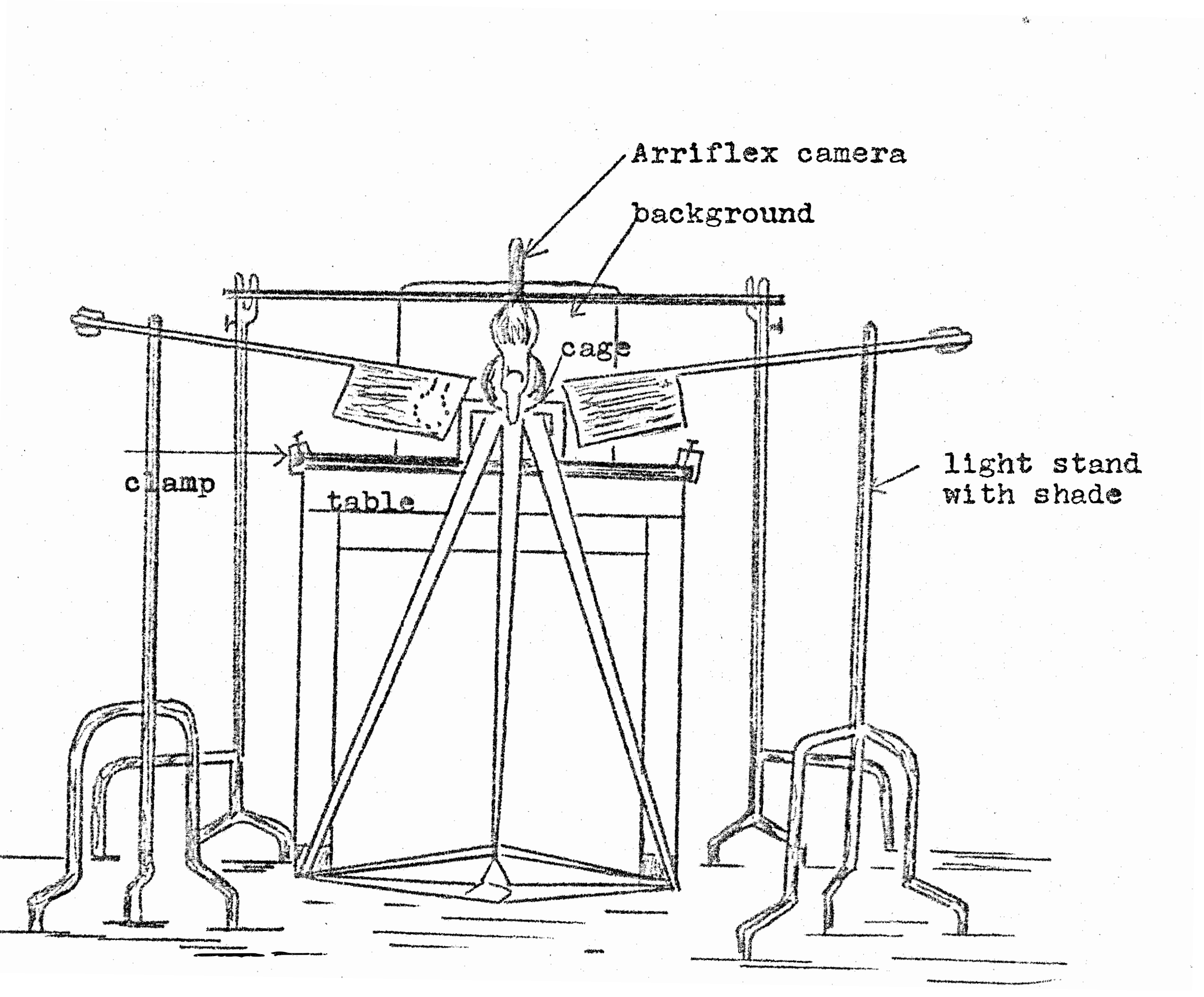
the cinematography lab: a) The clamps were loosened and the cage was taken off of the table. b) The moths present in the cage were carefully removed and kept for observation. c) The interior of the cage was washed with distilled water and the front glass cleaned. d) The piece of cheesecloth covering the back screen of the cage was removed and rinsed throughly in distilled water and put back over the screen. e) The cage was reclamped to the table. f) The moths were carefully injected into the cage through a hole in the back screen. g) Adjustments were made with Arriflex movie camera lens and preparations made for filming the moths.

The temperature in the cinematography lab was kept at 18°C. The two 25-w red bulbs raised the temperature in the cage to 23°C. The photographic set-up is shown in Figure C.

The following is the technical data regarding the cinematography.

Equipment:

16 mm Arriflex Camera model M, with 400 feet magazines; lens, Zoom 12-120 mm Angenieux F.T. stop 2.5 with 2 close-up lenses No. 1 and No. 2 Diopter.



The photographic set-up

FIGURE C

Lighting:

For infrared cinematography - 2 lamphouses were used each with 3 reflector-cone type 150-w bulbs wired in series and connected to 110v A.C. line

Large size (special order from Kodak) of Kodak Wratten filters No. 89B, with wavelength from 700 to 950 mu. were placed in front of light units.

For regular cinematography - 2 red bulbs of 25-w's each were set (one on each side) at a distance of approximately 8 inches emitting a total of about 30 foot-candles.

Film Stock:

Two kinds of film stock were used:

Kodak High-Speed Infrared Film - Approximate speed to tungsten light 200 ASA.

Kodak E.F. Color Reversal Film - type B with 125 ASA.

Exposure:

Twenty-four (24) frames per second - shooting F.T. stop of around 2.8.

Processing:

For the color film, processing was pushed by one half of stop.

Three naturally occurring geographical strains of the European corn borer from Minnesota, New York, and Wisconsin were crossed. Males and females from each strain were crossed with females and males of the other strain.

August 14, 1972 New York females were caged with Minnesota males, and when no matings occurred after 10 hours, the moths were left in the studio overnight with the lights on. The lights were turned off the next day and observations repeated. The females appeared to "call" and the males flew about the cage but did not extend their abdomens.

In succeeding crosses the moths were conditioned for three days, reversing night and day before caging together was attempted.

IV

RESULTS

Once the moth began to emerge from the pupal case, it took 14-17 minutes for the imago to expand and dry its wings. Figure D shows the stages of a healthy female moth from emergence to fully dried wings. Callahan (1965) states that in the corn earworm moth, it takes 17 minutes for the wings to expand and dry.

When a mating was successful it took two minutes on the average for the male to "dance" and mate with a receptive female. Figure E shows the actual mating sequence. The following are the usual behavioral characteristics of a successful mating in the cage.

a. The male has much antennal movement,

b. The male's wings extend upward and vibrate rapidly.

c. The male extends his abdomen.

d. The claspers begin to separate.

e. As the female advances, the male follows. This may happen several times.

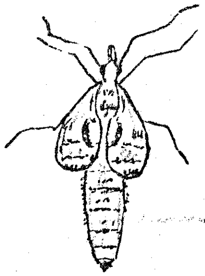
f. The heads of the male and female face in the same direction, the male to the rear.

g. The male twists abdomen forward to contact the female's genitalia.

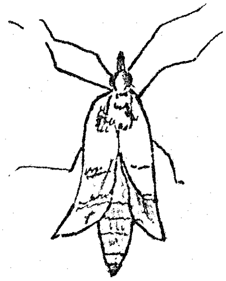
h. The female's abdomen extends slightly.

i. The male tries copulating again.

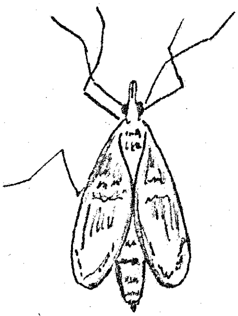
j. The mating is successful.



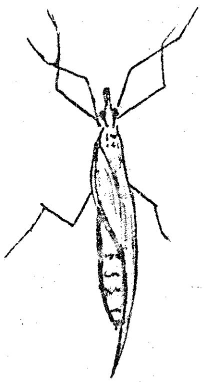
2 MINUTES AFTER EMERGENCE



13 MINUTES



15 MINUTES



17 MINUTES

FIGURE D

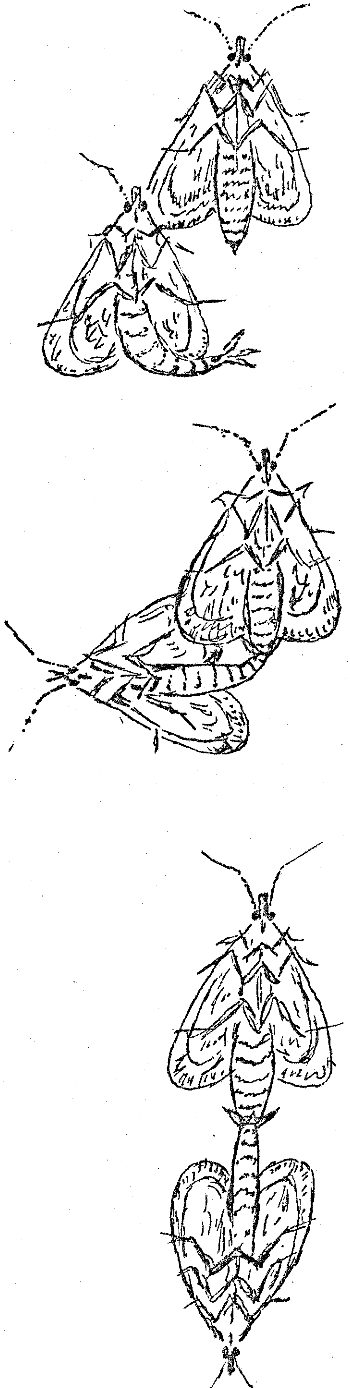


FIGURE E

k. When the genitalia are juxtaposed, the female remains quite passive.

l. The male and female then face in opposite directions.

m. The female moves pulling the male around with her.

n. The male appears tired and moves very little. His antennal movements are reduced.

o. The length of copulation lasts anywhere from 5 minutes to 2 hours.

p. Separation of the male and female appears to be very sudden and was not preceeded by any change in behavior.

q. The separated pair usually flew away from each other. Female usually flew to one corner of the cage and the male flew to some other part of the cage.

r. The female's abdomen made a pumping action and the male's claspers remained partially spread for a time.

In one case, three pairs of moths were put in the observation cage. When one pair mated they were marked by placing a black dot on their right wings. This pair did not mate the next day. On the third day, the same pair mated again even though they were still among other male and female moths.

Gently fanning the cage caused the males to begin precopulatory behavior often resulting in a successful mating. It would follow that in the field, a slight breeze would likely increase the number of matings.

It was found that different geographical strains of the European corn borer from Minnesota, New York, and

Wisconsin will mate when put together. (Table I) shows the results of the crosses. Since all of the crosses made between Minnesota, New York, and Wisconsin were successful, the sex attractant is not an individual isolator but is functional for the organisms used in this study. However, the first attempt to cross New York females and Minnesota males did not result in observed matings. A possible explanation is discussed later.

MOTHS CROSSED	DATES CROSSED	NUMBER OF MOTHS	MATING SUCCESS	NUMBER OF MATINGS
MINNESOTA MALES	OCTOBER 26	5	yes	3
NEW YORK FEMALES		6		
NEW YORK MALES	AUGUST 16	8	yes	1
MINNESOTA FEMALES		6		
NEW YORK MALES	AUGUST 17	6	yes	2
WISCONSIN FEMALES		6		
WISCONSIN MALES	AUGUST 18	6	yes	1
MINNESOTA FEMALES		5		
WISCONSIN MALES	AUGUST 21	6	yes	1
NEW YORK FEMALES		6		
MINNESOTA MALES	AUGUST 22	5	yes	1
WISCONSIN FEMALES		6		

TABLE I

V

DISCUSSION

To study the European corn borer moths' mating behavior preliminary observations had to be made during the night and early mornings inorder to catch their pre-copulatory behavior, the actual mating, and the post-copulatory behavior. The use of cinematography provided a closer and more accurate picture of the moths' behavioral characteristics.

By reversing the moths' day-night schedule it was possible to perform the cinematography work during the day in a darkened studio. One of the objectives of this research was to see if crosses could be made between Minnesota, New York, and Wisconsin European corn borer moths.

The first attempt to use infrared film as recommended by Sparks and Facto (1966) was not successful. It was found that too much heat was given off by the six 150-w cone reflector lamps needed with the infrared filters. The temperature inside the cage rose to 47°C and the moths died.

Two 25-w red bulbs were used next to illuminate the cage. This lighting proved to be most adequate and gave 30 foot-candles of light. Color film could then be used which simplified photographing and processing and reduced the cost of developing color film compared to infrared film. The color film gave much better definition than the IR sensitive film.

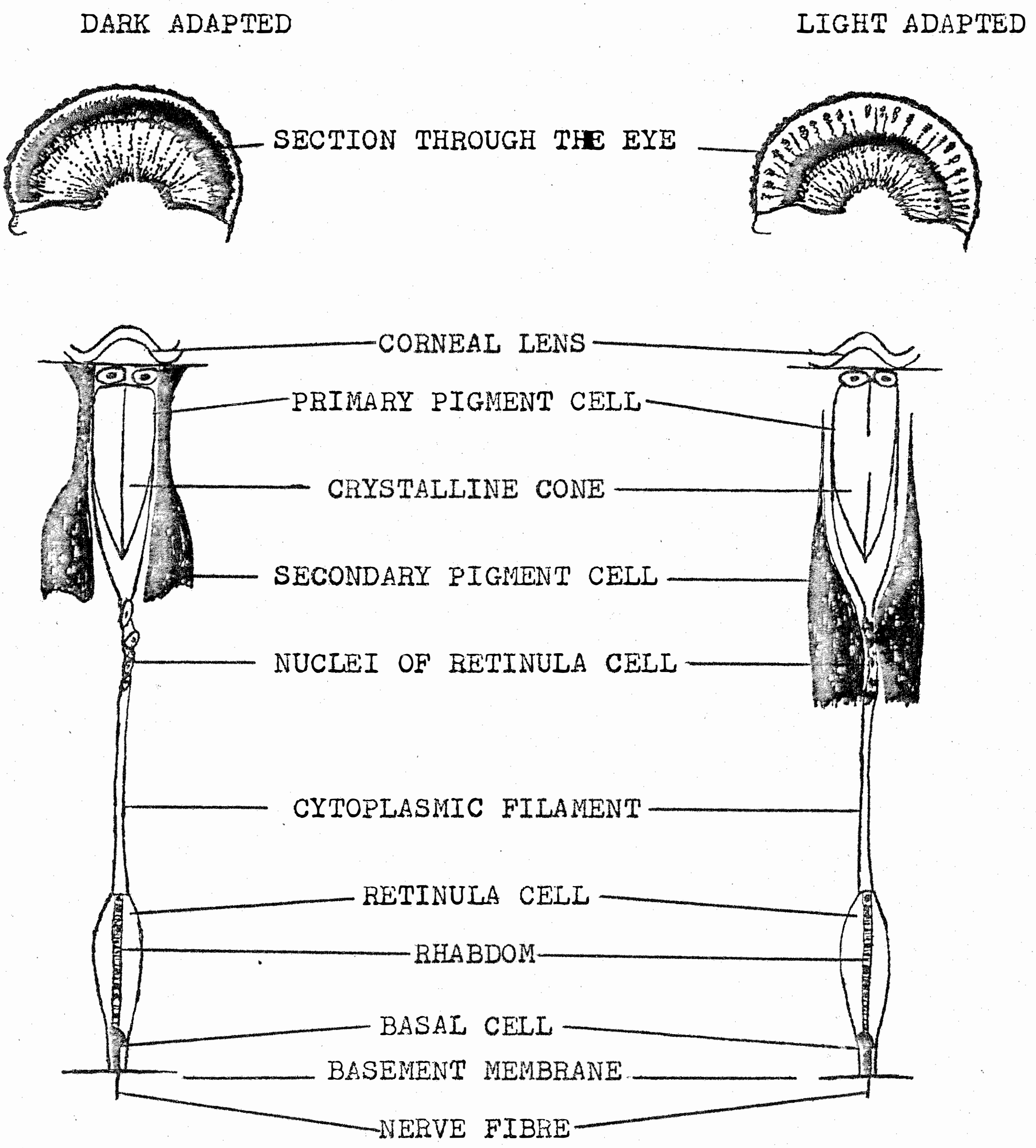
A suitable cage had to be constructed for the cinematography work. The cage had to be large enough to allow the moths room to move but small enough to photograph the entire inside of the cage on wide angle shots. The cage also had to be built so the moths would be seen at all times wherever they might be located inside the cage. The cage was fastened to a board and the board clamped to a table so that the cage would not accidentally be moved out of focus during filming.

The male moths are able to recognize the female by a sex pheromone, cis-11-tda (Klun and Brindley, 1970, Klun and Robinson, 1971), which she releases from the ninth and tenth segments of her abdomen (Drecktrah and Brindley, 1967). The male moths are able to position themselves to the side of the female where they appear to stroke her wing and abdomen with their front legs and antennae. The male moths were often confused and tried to copulate with other males to the extent of actually placing their claspers around the abdominal tip of the other males. Dustan (1964) mentions that on certain occasions the male Oriental Fruit Moths became so excited that they locked their own genitalia firmly together. In one case, this writer noted a male trying to mate with a female already in copulation. This male stood on top of the male in copulation and attempted to mate with the female. The attempt at mating with a male only came after a female released the pheromone in the cage. The pheromone stimulated the males to the point that they would often mistake a male for a female and attempt copulation. Traynier (1968) points out that the Mediterranean Flour Moth made copulatory movements towards objects resembling scenting females or sources of the sex pheromone placed on objects. Traynier's source of the pheromone was the ground up abdomens of female moths. Since male moths made copulatory movements toward objects resembling scenting females their sight may be the basis for final recognition of a mating partner. The sex pheromone is definitely important in the male's orientation to the female. Callahan (1965b) has mentioned the possibility of infrared sensing as a means of locating the opposite sex for resultant mating. In a few instances matings occurred in the cages during the light period. If the pheromone was not present and infrared sensing not a means of orientation then perhaps sight plays a role in mating, especially at close range.

The antennae of the male moved alternately and rapidly when the pheromone was present. The antennae play a role in the male's orientation to the female. Klun found that removal of the male's antennae resulted in inability to respond to the pheromone (Klun, 1968). George (1965) states that if the antennae of the Oriental Fruit Moth were cut off, the moths did not respond to the pheromone.

Sight did not seem to play much of a part in the detection of the female moths by the males but, as mentioned, it may be a last resort type of detection. When the red light was on, the moth's eyes often appeared to glow. Callahan (1965c) states that perhaps the night-adapted eyes of moths are perfectly suited for picking up sources of infrared radiation such as that which might be radiated by another moth. He also mentioned the glowing effect the eyes had at night but did not seem to have during the day. There is a definite pigment migration from daylight to darkness and vice versa. Day (1941) gives detail of an ommatidium in light and dark adapted conditions (Figure J).

The sex pheromone appeared to function as a close-range sex stimulant and the males were excited and seemed



Section through the eye of Ephestia and detail of an ommatidium in light and dark adapted conditions.

FIGURE J

to orient themselves toward the vapor source (Klun, 1968). The females usually released the pheromone when they were situated near the top of the cage and the males followed her if she continued to move around in the cage. The volume of air beneath the female's abdomen must contain the concentrated pheromone helping the male's orientation, since the males approached the females from the rear. Traynier (1968) found this to be true with the Mediterranean Flour Moth.

When the female was releasing the pheromone, the tip of her abdomen was exposed and often a pumping action was observed. The abdominal motion often involved side to side motion as the sex pheromone was being released. This pumping action was noted by Loughner (1971). Usually, a short time after this, the males would become excited opening their claspers and would attempt to copulate with other females who were not receptive. If the female was not receptive, the tip of her abdomen would not be exposed or if it was exposed would not be at the proper angle so that the male could copulate with her. The female would move away from the male each time he tried to mate. In several instances, the claspers would be almost around her abdomen and she would pull away from the male just when it looked as if copulation had taken place. When the female was receptive, her abdomen was arched slightly upward lining up with the dorso-lateral swing of the male's claspers. The females pre-mating behavior remained quite passive while the male was most active. After locating the female, the male would appear to stroke her wing and her abdomen with his front legs and antennae, and if she moved, he followed her. This stroking action caused her to arch the tip of her abdomen in a slightly upward position. This helped her line up with the male's claspers, as mentioned by Fatzinger and Asher in their 1971 study of Dioryctria abietella.

The male's courtship begins with the wings extended upwards and vibrating rapidly, the genitalia extended, and finally the opening of the claspers. The male followed the female if she moved up the side of the cage. He would situate himself to the lower right or left side of the female's wing and swing his abdomen with claspers opened upward in an attempt to copulate. The male did a "dance" prior to copulation. He walked in a circular fashion around the cage as his wings vibrated rapidly and his claspers opened. The male antennae moved rapidly as he walked around the cage. Klun (1968) states that his excited stage lasted for several minutes before the male would rest. This writer observed the male's excited state to last better than thirty minutes in some instances.

Copulation only took place when the females were ready. In one case, three males attempted to mate with one female who was most unwilling to cooperate. Each male at one time or another had his claspers around the tip of the female's abdomen, but each time the female pulled away from the male. There were many attempts at copulation on the part of the males but few successful copulations since the females were not always receptive.

On a few occasions it was observed that the male had died while still attached to the female and she was dragging his body around the cage with her. The excitation that the male experiences may be traumatic and may result in death. It may be assumed that multiple mating will shorten the life expectancy of the male. Once the pair are in copulation they can be picked up and shaken without causing separation.

On some occasions air currents were set up in the cage by fanning and this caused the males to become excited and start their characteristic precopulatory behavior which often resulted in successful matings. The fanning action distributed the female's pheromone around the cage making it possible for the male to detect the presence of the scent. From this reaction it can be postulated that air currents are necessary for orientation and a slight breeze in the field will increase the number of matings.

Penetration of the aedeagus was impossible to observe. One could clearly see the claspers gripping the abdomen of the female but it was difficult to see penetration of the aedeagus. Callahan (1958b) has some excellent serial sections of the corn earworm, Heliothis zea (Boddie), showing the position of the aedeagus in the female. The following description of the aedeagus is taken from the work done by Drecktrah and Brindley (1967). "The aedeagus is a cuticular, tubular structure approximately 1.0 mm long and 0.3-0.4 mm wide surrounding the endophallus. Several groups of muscles are inserted on its outer surface. It is supported by a diaphragm, the anellus, which closes the posterior end of the abdomen. It possesses a small, posteriorly directed sclerite ventrad to the secondary gonopore at the tip of the aedeagus. Two lightly sclerotized arms extend from the sclerite along the lateral aspects of the aedeagus and appear to fuse at the anteroventral margin of the aedeagus." Figure G and Figure H show the male's reproductive organs. When the male and female are in

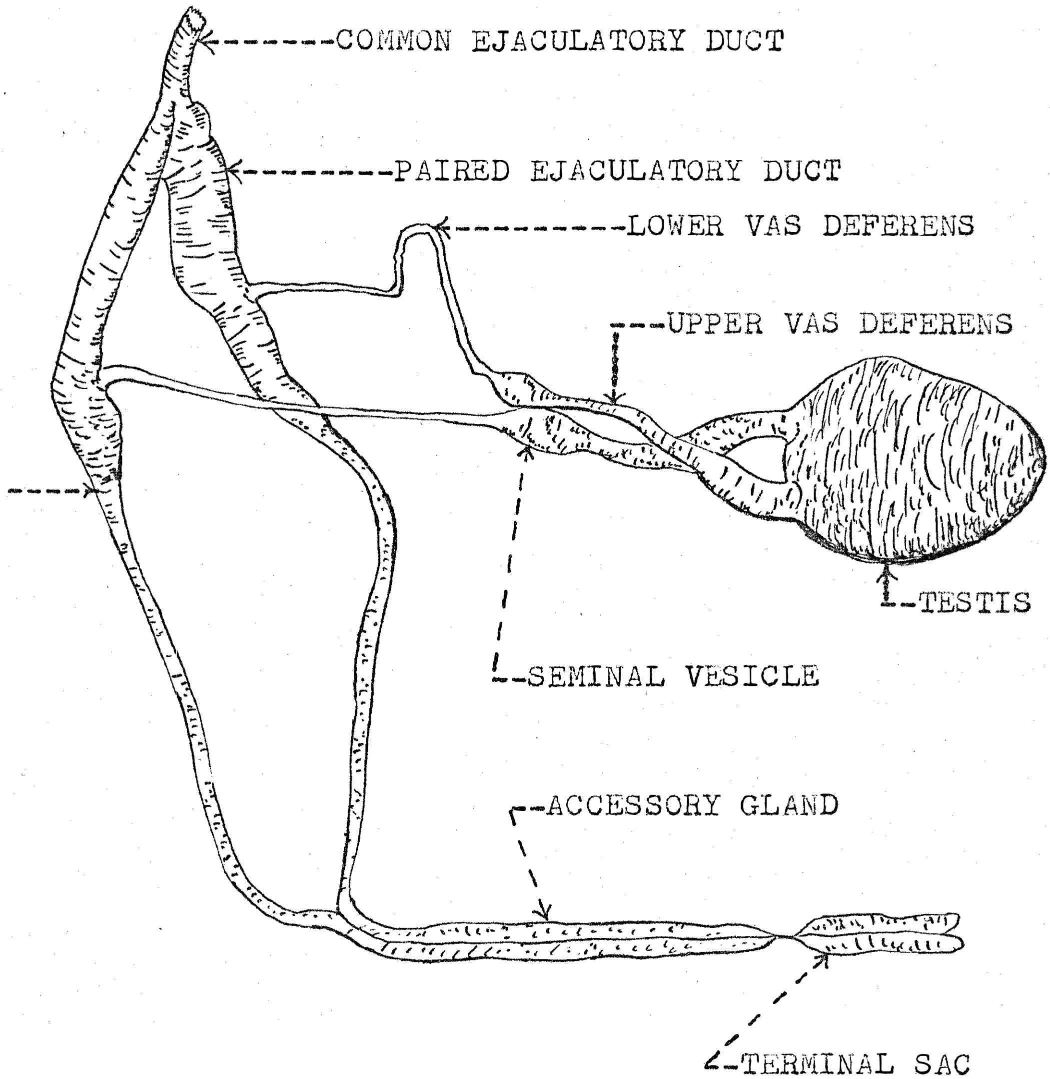

COMMON EJACULATORY DUCT
PAIRED EJACULATORY DUCT
LOWER VAS DEFERENS
UPPER VAS DEFERENS
TESTIS
SEMINAL VESICLE
ACCESSORY GLAND
TERMINAL SAC

FIGURE G

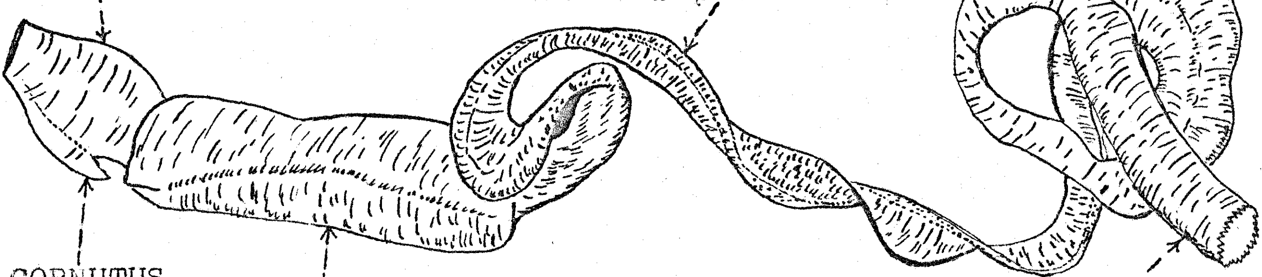

ENDOPHALLUS
COMMON
EJACULATORY DUCT
cuticular part
CORNUTUS
AEDEAGUS
COMMON
EJACULATORY DUCT
primary part

FIGURE H

copulation, the male transfers sperm by way of the aedeagus. The aedeagus penetrates as far as the bursa copulatrix of the female where a spermatophore is deposited.

Since the discovery of chemical sex attractants there is some evidence to support the hypothesis that the European corn borer moth could be attracted and/or inhibited by perhaps different sex pheromone released by geographically dissimilar females. If this is the case than there could be biological isolating mechanisms at work keeping different geographical strains from crossing. In a study done by Klun and Robinson (1971) it was found that cis-11-tda was a sex attractant released by the female to excite the male into precopulatory behavior but that trans-11-tda and 11-tdya inhibited the flight orientation of the European corn borer male. It has been found that cis-11-tda is also a sex attractant for the redbanded leaf roller (Roelofs and Arn, 1968). The redbanded leaf roller and the European corn borer moth have the same chemical sex attractant but do not mate. In a study done by Kaae, Shorey, and Gaston (1973), it was found that _Trichoplusia ni_, cabbage looper, and _Autographa californica_, alfalfa looper, are both attracted to cis-7-dodecenyl acetate. They demonstrated that the females release the pheromone at different rates which is the probable mechanism of reproductive isolation between the two species. The alfalfa loopers were caught in traps where the sex pheromone was released in low evaporation rates. The cabbage loopers were caught in traps where the sex pheromone was released in higher evaporation rates. Could this same type of mechanism keep the redbanded leaf roller from mating with the corn borer? Perhaps slight differences in their reproductive organs do not allow for copulation? It may also be possible that synergism plays a role in keeping the moths from crossbreeding. There may be two or more compounds which are vital to the moth's attraction to the sex pheromone even though these compounds might exist in only minute quantities. Research could be done to work on this type of problem using cinematography to record the behavioral actions. By utilizing chemical techniques related compounds to the sex pheromones could be synthesized and tested for male excitation. Peacock, Lincoln, Simeone, and Silverstein (1971) in their study with Scolytus multistriatus, concluded that there are two attractants which the elm bark beetle responds to. The beetles are attracted to a weak attractant from decaying elm tissue. As the beetles bore into the host there is increased volatilization of the host attractant. The virgin females first attracted by the host attractant produce a pheromone. The combination of the two attractants is responsible for the gathering of many male and female beetles. Klun and Robinson (1971) also found that although trans-11-tda and 11-tdya inhibited flight orientation in the European corn borer it did not inhibit precopulatory behavior and mating of the male.

In the crossing of Minnesota, New York, and Wisconsin strains, successful matings indicate that a chemical isolator to mating has not evolved. The failure of the first crossing of New York females with Minnesota males can be explained on photoperiodic response. Another explanation might be that since the moths were left together overnight in the lighted room matings occurred during this time and the next day no matings would occur.

Wisconsin females and Minnesota males were placed in the cage August 22. A single mating occurred this day. One male had his left front leg missing and he tried to mate several times with a female. Twice he was temporarily attached to her. Once he fell off of her near the top of the cage and once he was knocked off by another male flying around the cage. The lack of a front leg not only reduced his ability to achieve good footing but also presented a problem when he was trying to orient himself to the female during the mating act. Many times the males tried to copulate with the females but the females were not receptive and walked away from the males, or they did not present themselves to the males.

During the course of this research the following ideas for future study came to mind; Why do the moths wave their antennae so much? Does the alternate movement of the antennae help the male's orientation to the female? If one of the male's antennae were cut off, would this have an effect on the male and if so, what type of behavioral action would the male exhibit? If the female's antennae were cut off, would this cause a difference in her behavioral characteristics?

After a successful copulation it was observed that no other males bothered the mating couple except for the one case already stated. This writer wonders if the male might give off a pheromone which inhibits other males from attempting to copulate. Up to now the feeling has been that the female seems to be the only one that controls the male's mating behavior. Perhaps we should turn to the male to see if there is a male pheromone released during copulation. If this could be determined then perhpas there could be another means of control of this insect pest in corn growing areas.

VI

CONCLUSIONS

From the preceding results and discussion, it can be concluded that documentation of the precopulatory behavior, the actual mating behavior, and postcopulatory behavior of the European corn borer has been recorded on film through the use of cinematography.

Different geographical strains of adult European corn borer moths when crossed will mate, thus proving that the sex attractant is functional for the organisms used in this study (Minnesota, New York, and Wisconsin corn borers).

From the techniques and information obtained in this research project, it would seem evident that further investigations can be conducted using cinematography as an excellent tool to aid in the study of the European corn borer.

This author feels that the work accomplished in this research is important for the following reasons: The mating behavior of the European corn borer was well established and was permanantly recorded on film. This had not been completed before as far as the literature review shows. Techniques for filming the moths were developed so that future research work will have a foundation to build upon. The fact that Minnesota, New York, and Wisconsin male and female moths will successfully mate when crossed was documented. This writer found no reports dealing with the crossing of geographical strains of the European corn borer. All of the crosses made were recorded on film for further investigation and future work. This research leaves many unexplored avenues open to be worked on and developed.

If this writer were to continue studying the behavior of the European corn borer the questions posed in the discussion of this paper would first be investigated using cinematography to record the behavioral characteristics of the moths.

VII

SUMMARY

The mating behavior of the adult European corn borer moths was observed and recorded on film through the use of cinematography. This documentation includes precopulatory behavior, actual mating, and postcopulatory behavior. Many questions on the behavior of these moths were answered but the research led to many new questions which could be pursued.

Documentation was made of the crossing of geographical strains of Minnesota, New York, and Wisconsin male and female adult European corn borer moths. Their behavior was recorded on film and it was established that different geographical strains will mate.

VIII

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