DIAPAUSE INDUCTION AND SEASONAL ACTIVITY OF THE FACE FLY *MUSCA AUTUMNALIS* (DEGEER) IN OKLAHOMA

By

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(DEGEER) IN OKLAHOMA

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CHAPTER I

INTRODUCTION

Roubaud (1922, 1927) first noted that the face fly Musca autumnalis overwinters as an adult. Diapause in the face fly is characterized by hypertrophied ovaries, lack of mating, and increased development of fat bodies (Hammer, 1942; Pitts and Hopkins, 1965; Valder et al., 1969).

Saunders (1976) states that as the temperature is lowered and photoperiod shortened the percentage of insects in a population going into diapause increases. This conclusion agrees with the findings of Stoffolano and Matthysse (1966). Beck (1977) noted that combinations of thermoperiods and photoperiods strongly influence diapause determination. His dual system theory explains the existence of a S system (temperature controlled) and a P system (much less temperature sensitive) which are involved in determining the point at which an insect will enter diapause.

Caldwell and Wright (1978) reported that the critical photoperiod for diapause induction of face flies in Ontario to be 15 hours of light at a constant temperature of 16^{o}C in experiments conducted in the laboratory. The former corresponds with the natural photoperiod encountered by face flies in Guelph, Ontario. These results were obtained while using two colonies of face flies, one native to Ontario, the other a colony maintained for many years by Calvin Jones at

Lincoln, Nebraska. Results led the authors to postulate that because of constant rearing individuals in the Jones colony lost their ability to enter diapause under conditions that caused individuals in nature to enter diapause.

Geographical strains of an insect species have been investigated by a number of authors including Depner and Harwood (1966), Masaki (1961), and Tauber and Tauber (1972). Depner and Harwood (1966) found that strains of Anopheles freeborni from areas of different latitude had a one hour shorter critical photoperiod than the southern strain. Tauber and Tauber (1972) noted that a northern strain of Chrysopa carena had a one hour shorter critical photoperiod than the southern strain. Masaki (1961) reported that an introduced species responds as best it can to a new climate. Thus an introduced insect as the face fly must adapt to the conditions at hand in a given climatic area if the Masaki theory is correct.

This investigation was done to determine if a colony of northern face flies (North Dakota) had a critical photoperiod different than that of a colony of southern face flies (Oklahoma). In addition, a third colony (Jones) of long term colonization was compared. Wright (1970) suggested that the lack of diapausing insects in a colony of horn flies, Haematobia irritans, may have been caused by survival and thus selection of non-diapausing flies.

With this thought in mind during the present study I hoped by comparing the short term colonies (geographic strains) with a colony of long term colonization (Jones) a determination could be made whether long term colonization has affected the ability of insects to enter diapause. In conjunction with the laboratory study a field study was undertaken to observe the activity of the face fly in the field. Oklahoma is the limit of the southwestern range of the face fly and differences from observed activity in the north may be an indication of adaptations by the flies to exist in southern climates.

CHAPTER II

REVIEW OF LITERATURE

The face fly, *Musca autumnalis* DeGeer an introduced pest of livestock, was first recorded in Nova Scotia in 1952 (McNay, 1957, 1958). Since that time the fly has expanded its range to include Canada and a large part of the United States. The fly has been reported in every Canadian province (Depner, 1969), from Maine south to Georgia, west from West Virginia through Kansas and Colorado and north to the Canadian border (USDA, 1964). Since 1964 the face fly has expanded its range to include Arkansas (Boyer, Rouse, Lancaster, 1975), Mississippi (Mafes, 1975), Nevada, Utah (USDA Cooperative Plant Pest Report, 1977), California, Washington, Oregon and Oklahoma with the first reports of the species in these areas in 1969. The face fly probably entered Oklahoma in the northeast corner of the state where population densities are now highest and slowly expanded its distribution in a southwesterly direction.

One possible explanation for the slow increase in range in Oklahoma is the difference in habitat from eastern to western Oklahoma. The face fly needs moisture and shaded pastures to do well which are not as abundant in a prairie condition (Depner, 1969) and most extensions of range are restricted by a geographical barrier and climate restrictions (Messenger, 1959) which may be a factor in Oklahoma.

The economic loss to cattlemen caused by face flies has not been measured directly but losses due to irritation to cattle and loss in feeding time has been suggested (Benson and Wingo, 1962; Ode and Matthysse, 1967; Teskey, 1969). A USDA publication (1965) estimated that the face fly has cost the producer $68,000,000 over 10 years. Of this $42,000,000 was estimated to be the result of weight losses and $26,000,000 was attributed to losses in milk production.

The face fly annoys livestock by congregating around eyes and the nose, feeding on the mucous secretions or on wounds left from blood sucking flies (Hammer, 1942; Teskey, 1969). The cattle will huddle together, heads in the center of the circle or seek shelter to escape the flies. This supposedly causes a loss of feeding time along with the general annoyance of the flies. Parrish and Gerhardt (1976) noted that the number of flies on cattle was more affected by the cattle's movements to and from shaded resting places than by environmental factors. This contradicts Hammer (1942) who concluded that light and temperature were the most important factors affecting the number of flies on cattle. However, Benson and Wingo (1962) reported a 54% greater fly density on resting cattle which would seem to support the thoughts of Parrish and Gerhardt (1976). Treece (1960) stated that face flies were most active on cattle on sunny days.

The life history of the face fly has been well documented by Benson and Wingo (1962), Hammer (1942), Teskey (1960, 1969) and Wang (1964). These authors reported that the adult flies mate at three to seven days of age. Male flies will mate repeatedly, six to 13 times, whereas females will mate only once (Teskey, 1960, 1969). However, Wang (1964) reported that females mate at four to five days of age and two to three times. The initial ovarian cycle requires five days with all subsequent cycles being completed in two to seven days. Turner and Hair (1967) reported the importance of protein in the diet of the face fly for proper egg development. Bovine manure is the most common oviposition medium although swine (Fales et al., 1962) and bison manure (Burger and Anderson, 1967) have been reported as possible oviposition sites. Face flies usually deposit their eggs in the first three hours after an oviposition medium was made available (Teskey, 1969), although Hammer (1942) observed flies ovipositing in dung that was 24 hours old. How long an oviposition medium will remain attractive for oviposition depends on temperature, cloud cover, humidity, and the amount of wind (Hammer, 1942; Teskey, 1960, 1969). When the manure develops a crust that the flies ovipositor cannot pierce it then becomes unsuitable for oviposition. The eggs hatch in 24 hours and larvae burrow into the manure and remain in the pat for five days, pupate and emerge in approximately eight days post-pupation. At optimum conditions face flies may complete their life cycle in two weeks with a maximum life expectancy of three weeks to three months (Teskey, 1960, 1969; Wang, 1964).

Beck (1963) defines diapause as a state of arrested development in which the insect's respiration and metabolism has been suppressed and arrested morphogenesis and gametogenesis. Diapause may take place in any stage of development; egg, larvae, pupal, nymphal, or adult (Lees, 1955). Beck (1977) states that diapause is a combination of a dual system. The "S" system is involved in temperature sensitivity and the "P" system is sensitive to photoperiods and diapause is a response to both.

Diapause is generally confined to one stage in the insect's life cycle but there are exceptions (Lees, 1955). Insects which diapause as eggs, larvae, or pupae generally completely arrest development. Some insect species will enter diapause in every generation due to climatic or genetic factors and are termed obligatory (Beck, 1968). Other insects such as the face fly will enter diapause only if specific thermoperiods and photoperiods are present. This type of diapause is termed facultative.

Insects that diapause may be divided into two groups. Short day insects develop at short photoperiods into adults which lay normal eggs and will diapause in response to the lengthening photoperiod. Long day insects develop naturally at long photoperiods and will diapause in response to shortening photoperiods (Lees, 1955). The face fly is an example of a long day insect (Stoffolano and Matthysse, 1967).

Critical photoperiod is the photoperiod at which diapause is induced. There are many factors such as temperature, humidity, light intensity and age of the insect which influence the critical photoperiod. When computing the critical photoperiod, twilight must be considered. Insects have been shown to be sensitive to light levels as low as 5 lux (Danilevsky, 1965) which indicates that the low light levels of twilight may be important. The level of light intensity which influences diapause in the face fly as well as the importance of twilight in stimulating diapause has not been investigated.

Because the photoperiod varies geographically, a species with a wide distribution may develop into different strains with respect to its ability to enter diapause. The variation in photoperiod in the northern clines is much greater than that of the southern clines.

Depner and Harwood (1966) compared two strains of *Anopheles freeborni* Atkins from different latitudes. A one hour difference in the critical photoperiod for diapause induction was found between the California strain (southern) with a photoperiod of nine to ten hours required and the Washington strain (northern) with a required critical photoperiod of 11 to 12 hours. Danilevsky (1965) noted the Lepidopteran, *Acronycta*, which has a wide geographic distribution, had a critical photoperiod for diapause induction that varied with the different clines. The critical photoperiod varied from 20 hours in the north to 14.5 hours in the southern regions or about one hour for each 3^{o} latitude. Masaki (1961) stated that a one hour and 30 minute increase in critical photoperiod could be expected for each $5^{o}C$ decrease in temperature. Tauber and Tauber (1972) found a one hour critical photoperiod difference in the photoperiods inducing diapause in northern and southern colonies of *Chrysopa carnea*.

The face fly enters diapause as an adult (Hammer, 1942) and exhibits normal responses for an insect that enters facultative diapause. The characteristics seen in an adult in facultative diapause are: developed fat bodies in both males and females, lack of ovarian development in females, and no mating (Stoffolano and Matthysse, 1967). Pitts and Hopkins (1965) found that the fat content of diapausing flies was seven times that of non-diapausing flies.

Valder et al. (1969) reported that the face fly could be stimulated to enter diapause only in the first 24 hours after ecdysis. Further exposure to conditions stimulating diapause will only increase the intensity of diapause. Stoffolano and Matthysse (1967) reported that it was possible that both photoperiod and temperature were involved in inducing diapause in the face fly. Beck (1977) states thermoperiod and photoperiod are involved in stimulating an insect to enter diapause, but that thermoperiod may be more influential.

Face flies have been found overwintering in farm houses (Benson and Wingo, 1962), in old buildings (Teskey, 1969), attic and roof spaces (Dobson and Matthew, 1960) and in old garages (Caldwell and Wright, 1978). Hammer (1942) suggested that the face fly overwintered in hollow trees but this has never been confirmed. It has also been noted that the flies seem to go to the same overwintering sites each year. Stoffolano and Matthysse (1967) suggested that accumulation of fly specks or other attractants as a possible explanation for the return to the same overwintering sites. In the spring the flies emerge and mate. The females then go to the fields leaving the males near the overwintering spot to die (Benson and Wingo, 1962; Caldwell and Wright, 1978).

Stoffolano and Matthysse (1967) and Caldwell and Wright (1978) found a difference in diapause inducement in males and females. Stoffolano and Matthysse (1967) found highest inducement at 65^{o}F and total darkness and concluded that both temperature and photoperiod are important. This agrees with Caldwell and Wright (1978), however, Valder et al. (1969) reported that temperature is more important in inducing diapause. At 27^{o}C under varying photoperiods (zero to 16 hours) more than 90% of the females developed eggs. At 16^{o}C and a 12 to 16 hour photoperiod there was a much higher incidence of diapause. Caldwell and Wright (1978) achieved a higher percentage of flies entering diapause under varying temperature and approximating fall conditions than at all other temperatures and photoperiods.

Valder et al. (1969) had similar results and thus both groups agree that a simulated fall environment will stimulate diapause in the face fly better than artificial lab conditions.

CHAPTER III

MATERIALS AND METHODS

Colony Origins

Four colonies of face flies from different geographical origins were used in the experiments throughout the studies. The Oklahoma colony were offspring of face flies collected in the fall of 1977 from northeastern Oklahoma. The North Dakota colony was obtained from Dr. R. Meyers of North Dakota State University, Fargo, North Dakota. These flies were offspring from wild flies collected near Fargo in the fall of 1977. The Jones colony was also obtained from Dr. Meyers and is a colony of long standing colonized by the USDA in the mid-1960's. The Arkansas colony was also of long standing and was obtained from Dr. Lancaster of the University of Arkansas. This colony was from colonies at Purdue University and Kansas State University that periodically had some wild type flies from Arkansas introduced into it.

Stock Colony Rearing Conditions

All colonies were maintained in the Insectary at a temperature of 25-28^{o}C and a relative humidity of 50-70%. Both fluorescent and incandescent lighting were provided for illumination utilizing a 16/8 hour photoperiod.

Adults were maintained in cages (50x56x50 cm) constructed of fiberglass screen over a wooden frame. Nylon sleeves (15 cm diameter x 25 cm length) were used to provide access to the cages. Flies were provided free access to water from 4 x 10 cm bottles containing a cheese cloth wick. Food was provided as mixed dry diet in standard petri dishes and consisted of two parts nonfat powdered milk, one part powdered whole egg, and one part white granulated sugar. The diet was refrigerated until use to retard spoiling. Fresh bovine manure was used as an egging substrate. Manure was placed in round plastic pans (10 cm diameter) and offered to the flies at six days post-eclosion and every three to four days thereafter. Manure was left in the cages for twelve hours and then transferred to round pie pans (25 cm diameter) filled with manure. These pans were then placed in plastic pans (30 cm diameter) with 3 cm of sand in the bottom. The larvae were allowed to develop to maturity in the manure, at which time they crawled out and dropped to the sand and pupated. Pupae were sifted from the sand at three to four days post-pupation and then used to replenish stock colonies or in the experiments.

Experimental Chamber and Lab Exposure Technique

All laboratory studies were conducted in two Sheer environmental chambers (Cel® 37-14). Both fluorescent and incandescent lights were provided and the temperature was controlled via a programmable rheostat. Approximately 200 five to six day old pupae from each colony were placed in 30 x 30 cm (diameter) round cages constructed of a woodstock with fiberglass screen over the stock and a nylon sleeve in one end to provide access to the cage. They were then placed into the chambers at a predetermined photoperiod-temperature combination. All flies emerged under exposure conditions and were provided free access standard laboratory diet and water. Flies remained in the cages until dissection, at which time they were collected using a Sears SPV® vacuum fitted with 1¼ x 4 inch Drosophila culture tubes (Carolina Biological Supply) with a screened end.

Diapause Criteria and Dissection Technique

The criteria used to differentiate between diapausing and non-diapausing flies were the following: fat body development in both males and females, absence of sperm in spermetheca, and lack of ovarian development in females (Caldwell and Wright, 1978; Stoffolano and Matthysse, 1967).

Flies from each cage were collected and killed. Fifty males and 50 females were separated and placed on a 10 cell Boerner microscope slide (57 x 108 mm). Flies were then dissected under a Baush and Lomb® Sterozoom microscope (1x to 7x) by opening the abdomen with dissection forceps. The presence of or lack of fat body was observed and recorded. In females the ovaries were observed and the developmental state of the ovaries recorded.

The spermatheca was removed by applying pressure to the abdomen which forced the extension of the ovipositor. The ovipositor was then grasped with forceps and slowly pulled out to expose the three spermatheca. These were removed and placed on a 2.5 x 7.5 cm microscope slide and viewed under an AO Spencer Phase Star® microscope at 100x and the presence or absence of sperm recorded.

Preliminary Study

Oklahoma and Arkansas flies were exposed to four photoperiods and two temperatures. Both colonies were subjected to all eight combinations of temperature and photoperiod. The photoperiods used were 12/12, 13/11, 14/10 and 15/9 hours, light/dark. Temperature was maintained at 21^{o}C or 27^{o}C. Cages containing pupae from each colony were placed in the chambers at the prescribed temperature-photoperiod combination.

In the first experiment, cages of flies from each colony were removed at seven days post-emergence and returned to the Insectary for seven days. Fifty males and 50 females from each cage were dissected at 14 days post-emergence. In the second experiment flies from each colony were placed in the chambers at the desired temperature-photoperiod combination for 14 days post-emergence. They were then removed and 50 of each sex were dissected to note percent diapause.

Comparison of Diapause Induction of Flies of Different Geographical Origins

Flies from the Oklahoma, Jones, and North Dakota colonies were used in this experiment. Four photoperiods of 12/12, 13/11, 14/10, and 15/9 hours were used. The temperature was maintained at 21^{o}C with two replications being completed at each photperiod. To determine the length of exposure time needed to stimulate diapause, flies were exposed to each photoperiod for seven, nine, 11 and 14 days post-emergence. The flies removed from the environmental chambers at seven, nine and 11 days were taken to the Insectary and reared until 14 days of age. At 14 days post-emergence 50 flies of each sex were dissected and percent diapause noted.

Fall Exposure

This study was designed to give information of colony responses under natural conditions stimulating diapause in the fall. Flies from North Dakota and Oklahoma colonies were used. Cages with pupae were placed in an outside screen house once weekly with first emergence on August 10, 1978. The screen house had four sides screened and a solid roof. Flies were dissected at 14 days post-emergence to note percent diapause. Temperature and humidity were monitored with a Serdex® RH and temperature recorder throughout the exposure periods. The study was concluded on October 26, 1978.

Fall Simulation

North Dakota, Oklahoma and Jones colonies were used in this study. Flies were exposed in the environmental chambers to photoperiods and temperature duplicating conditions of selected weeks during the fall (Table V). The temperature was varied by a cam operated rheostat controlling the rise and fall of the daily temperature cycle. High temperatures were reached at 1:00 to 3:00 p.m. and the low temperature at 3:00 to 5:00 a.m. Two cages of each colony were used in each replication. One cage was removed at seven days post-emergence and returned to the Insectary. The other cage was removed at 14 days post-emergence and both cages of flies were dissected to note percent diapause at 14 days post-emergence.

Field Studies

Three areas were used to monitor face fly emergence in the spring, population fluxuations during the summer, and the entrance of over-wintering sites after diapause induction in the fall. These areas were near Burbank, Oklahoma in Osage County, the OSU range west of Stillwater, Oklahoma in Payne County and near Pryor, Oklahoma in Mayes County. Beef herds were surveyed each week in each area. Trips to the survey areas began in mid-March and concluded in mid-October. One non-treated beef herd was surveyed each week. Approximately 20 head of cows were observed with binoculars and face flies counted on one side of the back and the face of each animal. Ten manure pats were collected at random from each site and returned to Stillwater each week. Emergence traps were placed over the pats and all emerging flies collected, identified and counted. Living flies were collected from each area whenever possible and dissected to note percent diapause in the natural population.

CHAPTER IV

RESULTS

Preliminary Study

Preliminary studies were initiated in the fall of 1977 utilizing colonies of face flies of two origins. Oklahoma flies maintained at a temperature of 21°C exhibited no distinct peak of diapause induction. The percentage diapause (Table I) at 21°C over the photoperiods tested were not significantly different $P > .05$[1]. Responses of the Oklahoma colony at 27°C did exhibit diapause induction. Peak diapause was observed at 12/12 with 61.7% of the flies in diapause. There was a smaller peak at 14/10 with 35.4% entering diapause. At both temperatures used, a variation between sexes was observed (Table I). In all but replication 1, 12/12 at 21°C, the percentage of diapausing males was greater than the percentage of females in diapause. The largest differences in percentage diapause induction at the same photoperiod were observed at the 13/11 photoperiod. At 21°C, 52% entered diapause while at 27°C, 4.1% of the Oklahoma colony flies entered diapause. Similar differences between the two temperatures can be seen at each photoperiod (Table I). Few of the Arkansas colony entered diapause at the conditions they were subjected to in this experiment (Table II).

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[1]SAS Oklahoma State University, designed and implemented by Anthony J. Barr and James H. Goodnight, Department of Entomology, North Carolina State University, Raleigh, North Carolina.

TABLE I

PERCENTAGE DIAPAUSE OF OKLAHOMA FACE FLIES EXPOSED TO FOUR PHOTOPERIODS AND TWO TEMPERATURES: FLIES EXPOSED FOR SEVEN DAYS AND MAINTAINED IN COLONY CONDITIONS FOR SEVEN DAYS

Colony	Replication	Photoperiod	Number Flies Dissected Per Sex	Temperature	Percent Male	Percent Female	Total	Average of Replications 1 & 2
Oklahoma	1	12	50	21°C	32	56	44	50
	2		50		48	64	56	
	1	13	50	21°C	66	52	59.3	52
	2		50		52	38	45.0	
	1	14	35	21°C	71.5	50	61.5	45.3
	2		50		28.8	30	29	
	1	15	50	21°C	43.6	42	43.2	31.5
	2		50		20	20	20	
Oklahoma	1	12	35	27°C	88	52	70	61.7
	2		50		58	48.6	53.7	
	1	13	50	27°C	2.3	0	1.1	4.1
	2		50		10	4	7	
	1	14	50	27°C	17	13	15	35.4
	2		50		50	61	55.9	
	1	15	50	27°C	14	11	13	18
	2		50		30	16	23	

TABLE II

PERCENTAGE DIAPAUSE OF ARKANSAS FACE FLIES EXPOSED TO TWO TEMPERATURES AND FOUR PHOTOPERIOD COMBINATIONS: FLIES EXPOSED FOR SEVEN DAYS AND DISSECTED AT 14 DAYS POST-ECLOSION

Colony	Replication	Photoperiod	Number Flies Dissected Per Sex	Temperature	Percent Male	Percent Female	Total	Average of Replications 1 & 2
Arkansas	1	12	50	21^oC	2	2	2	6.7
	2		50		17	6	11.3	
	1	13	50	21^oC	0	2	1	1.0
	1	14	50	21^oC	0	0	0	0.0
	2		50		0	8	4	
	1	15	50	21^oC	17.4	2	9.7	19.9
	2		50		32.5	28	30.3	

At 21°C the highest percentage diapause was 19.9% at the 15/9 photoperiod. Very few of the Arkansas colony flies lived at 27°C and all of these were at the 12/12 hour photoperiod. No determination of how many of the dead flies might have been in diapause was made since the criteria for diapause were based on the number of flies living at 14 days.

To determine if the experimental design of seven days exposure and the removal to standard condition for the next seven days exposure affected the results, a 14 day exposure was initiated. Both colonies were exposed at 21°C to the four photoperiods used previously. Differences between the seven and 14 day exposure in the Arkansas colony percentages of diapause were observed at 12/12 and 13/11 (14 day exposure) with 28% and 48% respectively (Table III) as compared to 6.7% and 1.0% at the seven day exposure (Table II). Oklahoma colony face flies showed a significantly higher peak at only one photoperiod, 13/11 with 92.4% (Table III) diapause at 14 days exposure as compared to 52.0% at seven days exposure.

Geographical Study

In the preliminary studies many flies died at 27°C and it was difficult to obtain sufficient numbers for dissection. Therefore, an intermediate temperature of 21°C which had been used in previous studies (Caldwell and Wright, 1978) was chosen as a temperature which would give the best comparison of photoperiods to determine differences between geographical strains of face flies.

Comparison of percentage diapause in both sexes of face flies of the Jones, Oklahoma, and North Dakota colonies over the range of

TABLE III

OKLAHOMA AND ARKANSAS FACE FLIES EXPOSED TO ONE TEMPERATURE AND FOUR PHOTOPERIODS FOR TWO WEEKS

Colony	Photoperiod	Temperature	Number Dissected Per Sex	Percent Male	Percent Female	Totals
Arkansas	12	21°C	50	10	46	28
	13	21°C	50	45	51	48
	14	21°C	No Data	0	0	0
	15	21°C	50	0	0	0
Oklahoma	12	21°C	50	54	48	51
	13	21°C	50	90.9	94.7	92.4
	14	21°C	50	46	34	40
	15	21°C	50	31.1	16	23.5

photoperiods is recorded in Figure 1. Each point on the figure represents 800 dissections. Peak induction for Oklahoma and North Dakota flies (55.4% and 38.6%, respectively) was at the 14/10 photoperiod. Jones colony flies exhibited their peak diapause induction (67.3%) at the 13/9 photoperiod.

Jones and North Dakota flies exhibited lowest diapause induction, 7.8% and 8.3%, respectively at 12/12 photoperiod while the Oklahoma flies lowest diapause induction (20.3%) was at the 15/9 photoperiod. There was not a significant difference ($P > .1$) between the northern colony (North Dakota) and the southern colony (Oklahoma) in regards to critical photoperiod (14/10) at 21^{o}C. However, a consistently higher number of both sexes of Oklahoma flies entered diapause throughout the studies. This difference was significantly higher ($P > .1$) when comparing Oklahoma male flies to North Dakota male flies but not the females.

The Jones colony critical photoperiod was determined to be at the 13/11 photoperiod. This was significantly different ($P > .05$) from the critical photoperiod of the North Dakota and Oklahoma face flies (14/10). This peak diapause induction at 13/11 with the Jones flies was also significant ($P > .05$) within colony comparisons over the photoperiod range.

Figure 2 shows the percentage diapause of the three colonies according to sex at each of the four photoperiods. In all colonies a significantly higher number of males entered diapause than females ($P > .001$). Both sexes, of a given colony, responded in a similar manner (Figure 2). Oklahoma and North Dakota flies responded in a similar pattern except at the 12/12 photoperiod.

Figure 1. Percentage Diapause of Face Flies from North Dakota, Oklahoma, and Jones Colonies at 21^{o}C and Four Photoperiods.

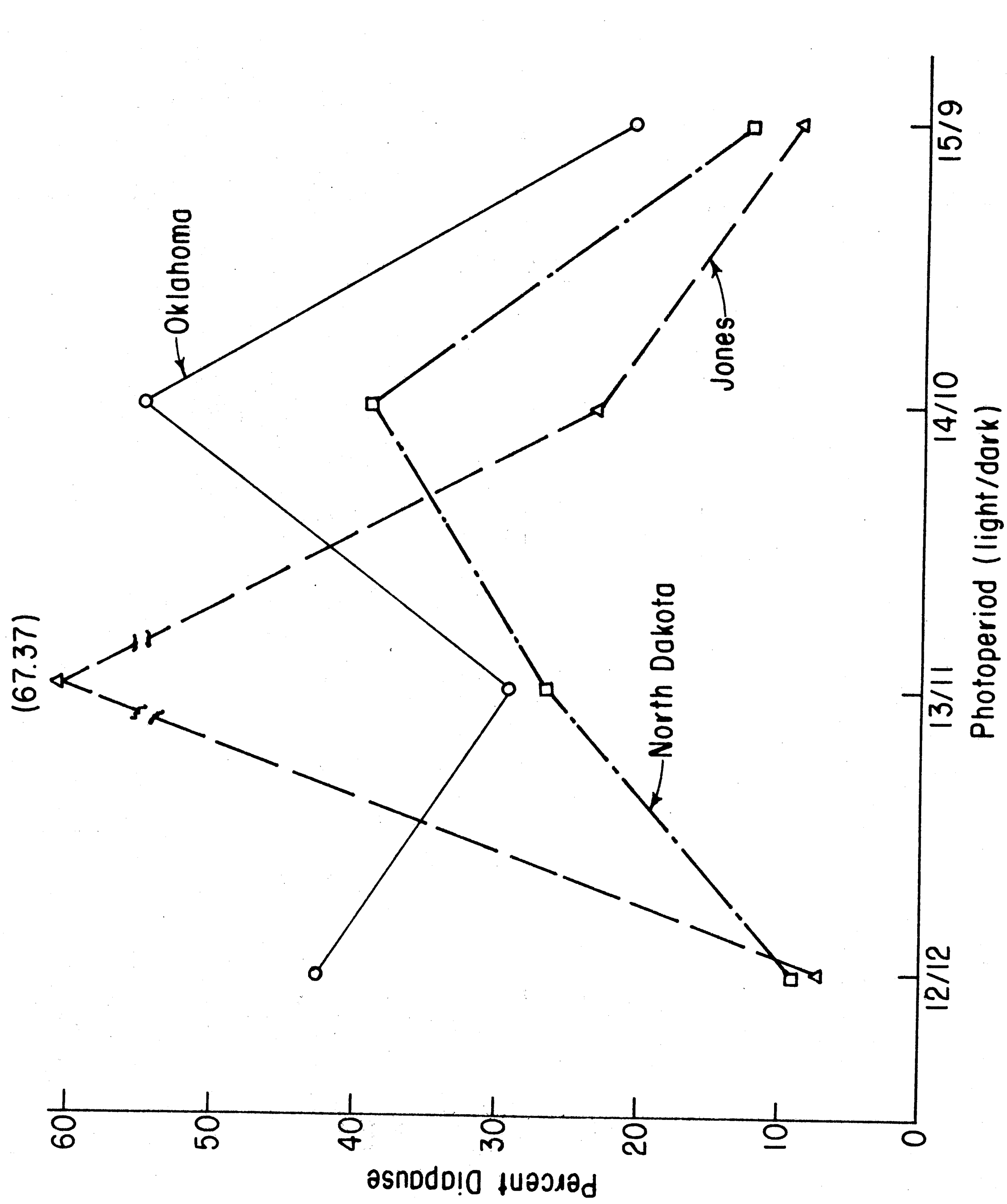
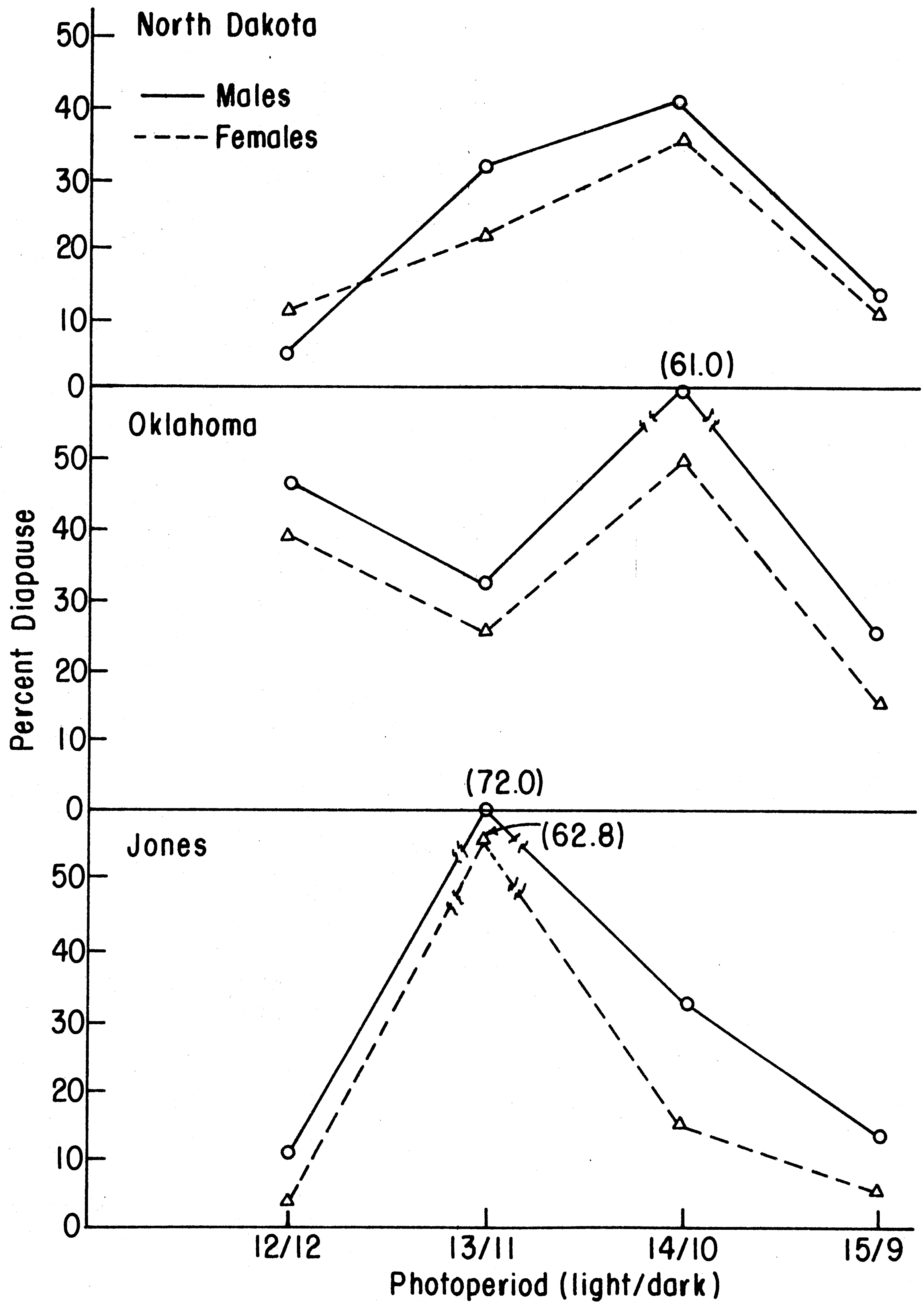

(67.37)
Oklahoma
North Dakota
Jones
Percent Diapause
0
10
20
30
40
50
60
12/12
13/11
14/10
15/9
Photoperiod (light/dark)

Figure 2. Percentage Diapause of Face Flies from North Dakota, Oklahoma, and Jones Colonies Divided into Sex at 21°C and Four Photoperiods.


North Dakota
Males
Females
Oklahoma
(61.0)
Jones
(72.0)
(62.8)
Percent Diapause
50
40
30
20
10
0
12/12
13/11
14/10
15/9
Photoperiod (light/dark)

The difference in diapause induction according to the number of days exposed to each photoperiod is shown in Figure 3. However, in the AOV of the days exposure, photoperiod x days and days x sex interactions all have a $P > .06$. This indicates that the number of days exposure does influence the percentage of flies entering diapause. All colonies showed an increasing number of flies entering diapause up to nine days exposure (Figure 3). However, exposure lengths of more than nine days did not seem to increase the number of flies in diapause.

Table IV gives data for the three colonies according to photoperiod, sex and days exposure. In most day-photoperiod combinations significantly more males entered diapause than females ($P > .05$). The highest percentage of flies (one cage) found to be in diapause was 72% of the Jones colony males at nine days exposure. The highest colony average over the photoperiods tested (days averaged) was in the Jones colony, 13/11 with 67.4% diapause.

Fall Field Exposure

Figure 4 shows the percentage diapause of North Dakota and Oklahoma colony flies when exposed to actual outside conditions from August 18 to October 26, 1978. Jones colony flies were also placed outside but due to high mortality were not analyzed. Each point on the figure represents the percentage of 100 dissected flies, 50 males and 50 females, that were in diapause. First diapause was recorded on September 1, 1978. The percentages of flies in diapause rose to 68% (North Dakota) on September 9 and to 79% (Oklahoma) on September 13 when the natural photoperiod was 15.5/8.5 hours. During the next

Figure 3. Percentage Diapause of Face Flies from North Dakota, Oklahoma, and Jones Colonies at Seven, Nine, 11, and 14 Days Exposure.

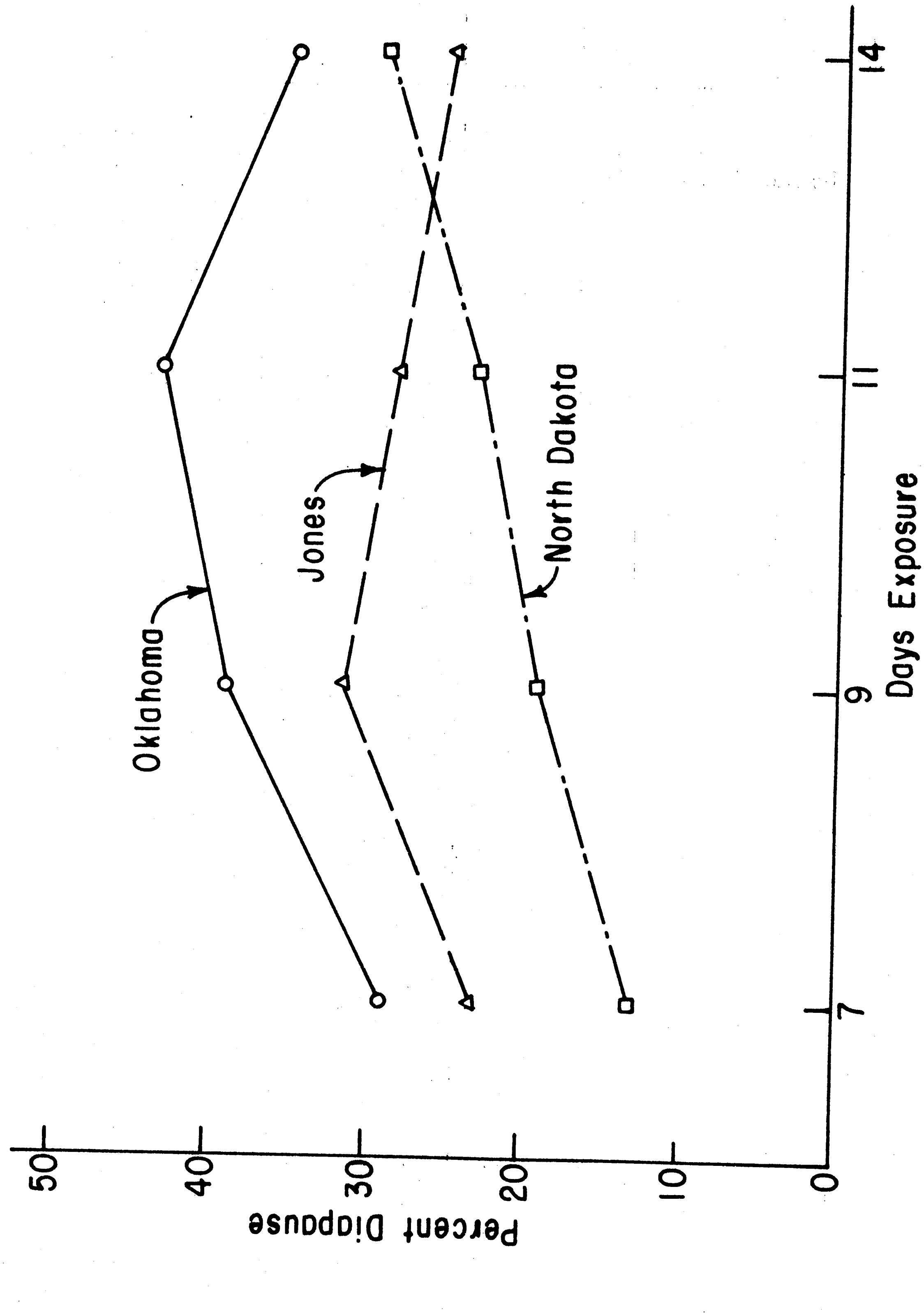

Oklahoma
Jones
North Dakota
Percent Diapause
0
10
20
30
40
50
7
9
11
14
Days Exposure

TABLE IV

PERCENTAGE DIAPAUSE OF NORTH DAKOTA, OKLAHOMA, AND JONES COLONY FACE FLIES WITH PHOTOPERIOD, DAYS EXPOSURE, AND SEX CONSIDERED

Photoperiod	Days	Sex		Percent Diapause Colony North Dakota	Oklahoma	Jones
12	7	Male		6	45	6
		Female		0	38	1
	9	Male		0	45	38
		Female		11	41	13
	11	Male		12	67	2
		Female		19	44	2
	14	Male		5	47	2
		Female		13	32	0
			Average Percentage Flies in Diapause*	8.3	42.4	7.8
13	7	Male		22	17	58
		Female		9	16	63
	9	Male		51	56	74
		Female		28	37	67
	11	Male		34	24	83
		Female		35	14	71
	13	Male		20	33	68
		Female		14	33	55
			Average Percentage Flies in Diapause*	26.6	28.8	67.4

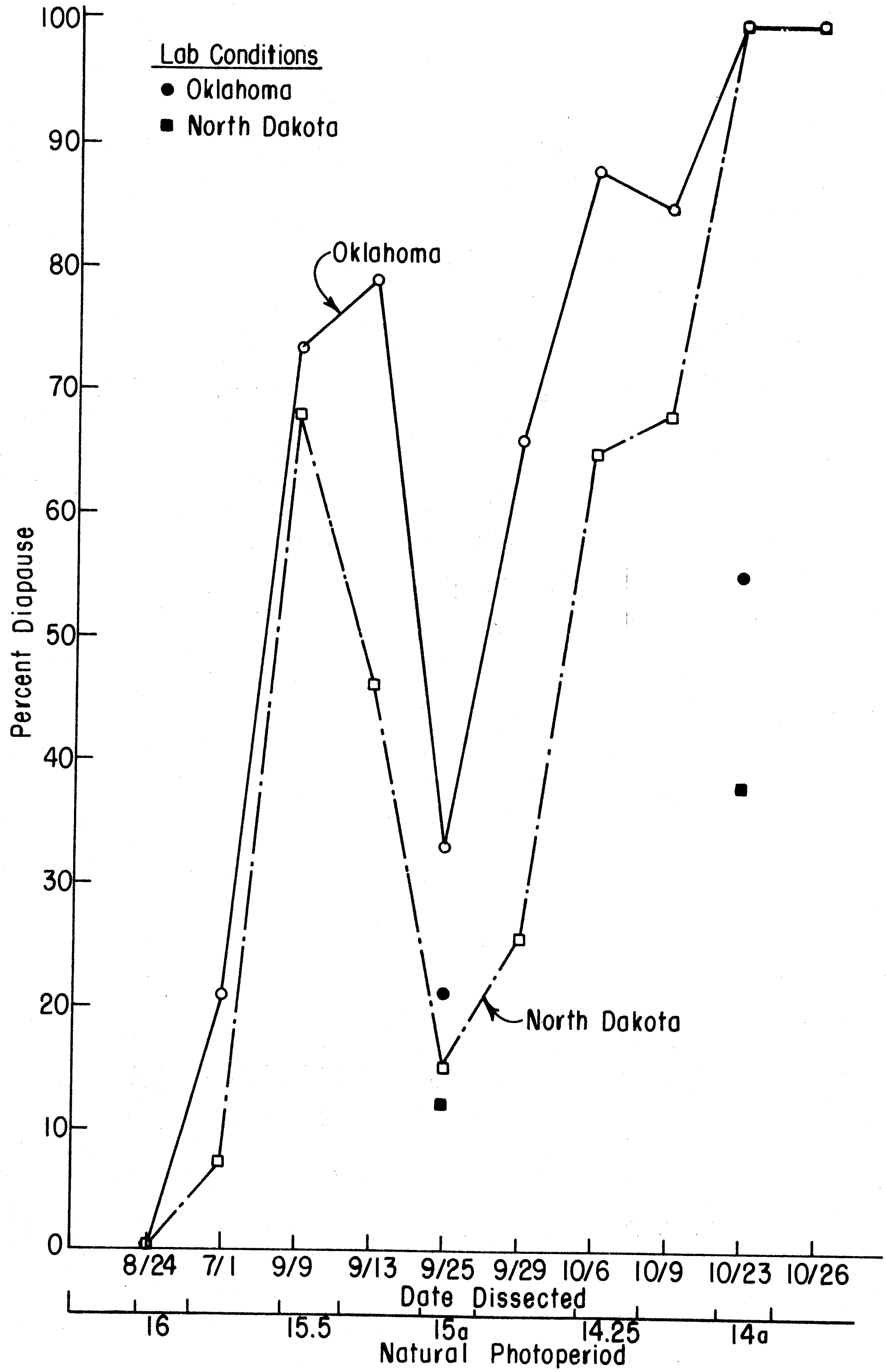
TABLE IV (Continued)

Photoperiod	Days	Sex		Percent Diapause Colony North Dakota	Oklahoma	Jones
14	7	Male		45	51	39
		Female		19	44	11
	9	Male		34	72	40
		Female		10	56	20
	11	Male		34	67	26
		Female		29	53	22
	14	Male		52	55	25
		Female		67.5	43	7
			Average Percentage Flies in Diapause*	38.6	55.1	23.8
15	7	Male		4	13	10
		Female		2	8	0
	9	Male		14	5	2
		Female		10	0	0
	11	Male		13	63	18
		Female		12	33	0
	14	Male		20	20	23
		Female		21	20	22
			Average Percentage Flies in Diapause*	12.0	20.3	9.4

*Percentages used on Figure 1.

Figure 4. Percentage Diapause of Face Flies from North Dakota, Oklahoma, and Jones Colonies Exposed to Natural Fall Conditions from August 18 to October 26, 1978.

a - Indicates photoperiod and results from laboratory exposure (Figure 1)



100
90
80
70
60
50
40
30
20
10
0
Percent Diapause
Lab Conditions
● Oklahoma
■ North Dakota
Oklahoma
North Dakota
8/24
7/1
9/9
9/13
9/25
9/29
10/6
10/9
10/23
10/26
Date Dissected
16
15.5
15a
14.25
14a
Natural Photoperiod

two weeks (September 13 to September 25) the percentage diapause dropped significantly (Figure 4). These percentages, 33% and 15% for the outside exposure in Oklahoma and North Dakota flies respectively, compare with 21% and 12% as the low percentage diapause observed in the laboratory at a similar photoperiod.

The percentage of flies in diapause from both colonies rose from September 25 until October 26 when 100% of the living flies were in diapause. One hundred percent of the flies dissected on October 23 from the field exposure cages at a photoperiod of 14/10 were in diapause while only 55% and 38% (Oklahoma and North Dakota, respectively) of the flies dissected from laboratory exposure at the same photoperiod were in diapause (Figure 4).

Flies placed outside after October 26 emerged and were left outside in actual late fall conditions. They were provided 10 cm x 10 cm x 6 cm wooden boxes as diapause sites. Observations made on December 2 found no observable living flies, however, the cages were left out all winter to determine if any flies would overwinter.

Simulation of Fall Field Exposure

Natural photoperiods encountered during the fall were used as the photoperiods in this laboratory study (Table V) of all colonies. Temperatures used were the ten year averages for this time of the year. Temperature was varied from the high to the low as stated in the Materials and Methods. These simulated conditions were determined to be as close to natural conditions as could be maintained with the resources at hand.

There was no diapause at the 16/8 photoperiod which was the

TABLE V

TEMPERATURE-PHOTOPERIOD COMBINATIONS, SIMULATION OF FALL FIELD EXPOSURE

Experiment	Date Imitated	Temperature		Photoperiod	
		High	Low	Light	Dark
1	August 23	32^{o}C	21^{o}C	16.25 hr	7.75 hr
2	September 7	32^{o}C	10^{o}C	15.5 hr	8.5 hr
3	September 22	26.5^{o}C	4.5^{o}C	15 hr	9 hr
4	October 7	26.5^{o}C	4.5^{o}C	14.25 hr	9.75 hr
5	October 17	21^{o}C	4.5^{o}C	14 hr	10 hr

Insectary rearing condition. The Jones colony flies had 100% diapause at the 15.5/8.5 photoperiod with a 32-10^{o}C temperature range and then had less than 25% diapause at all subsequent photoperiod-temperature combinations (Figure 5). The Oklahoma colony responded in a similar pattern as they did outside, with a first peak at 15.5/8.5 photoperiod with a 20% decrease at the 15/9 photoperiod and then an increase to greater than 75% diapause thereafter (Figure 5). The North Dakota colony flies had less than half the diapause induction under the laboratory simulated conditions than they had under natural conditions (Figure 5). The general pattern of diapause was similar to the pattern of diapause observed under natural conditions.

Field Study

Field observations were started on March 1, 1978 with first fly activity noted on March 22 when face flies were collected from overwintering sites in Osage County. These flies were found in two old medicine cabinets on the east wall of an old barn and resting on the outer walls of an old double walled grainery. Flies were also seen on one horse and one cow. Face flies were collected from a white frame house the following week.

Two areas were used for survey in Osage County. A dairy herd that was not treated was used for both survey and pat collection. A beef herd that was pastured on land adjacent to the dairy was used as a second survey herd. Flies were observed on animals from March 28 to October 4, 1978 (Figure 6). The highest fly/face ratio was recorded on June 29 with 26.1 flies/face on the dairy herd. The face fly population ranged from eight to 20 flies/face thereafter until

Figure 5. Percentage Diapause of Face Flies from North Dakota, Oklahoma, and Jones Colonies Exposed to Simulation of Natural Fall Conditions.

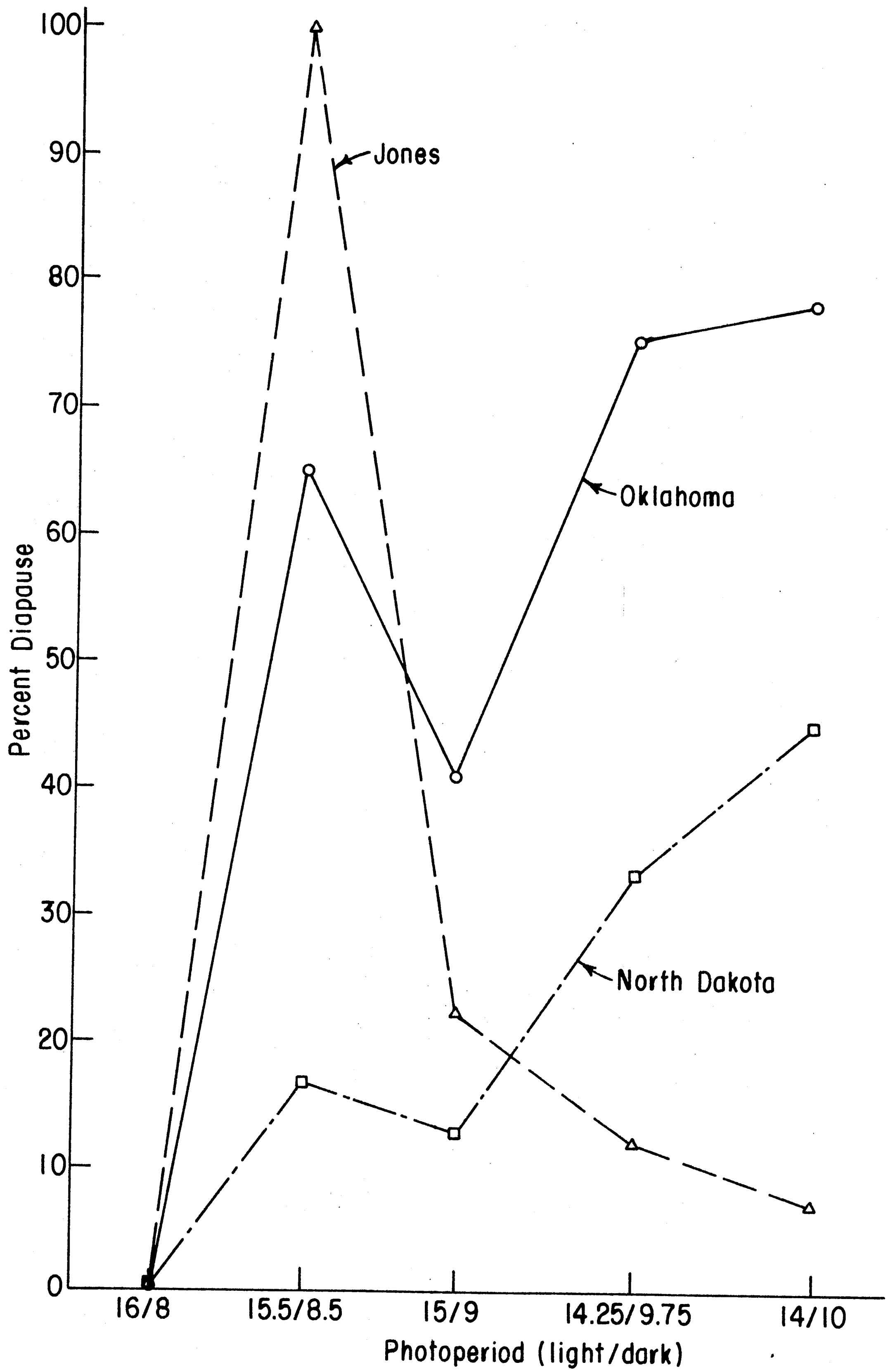
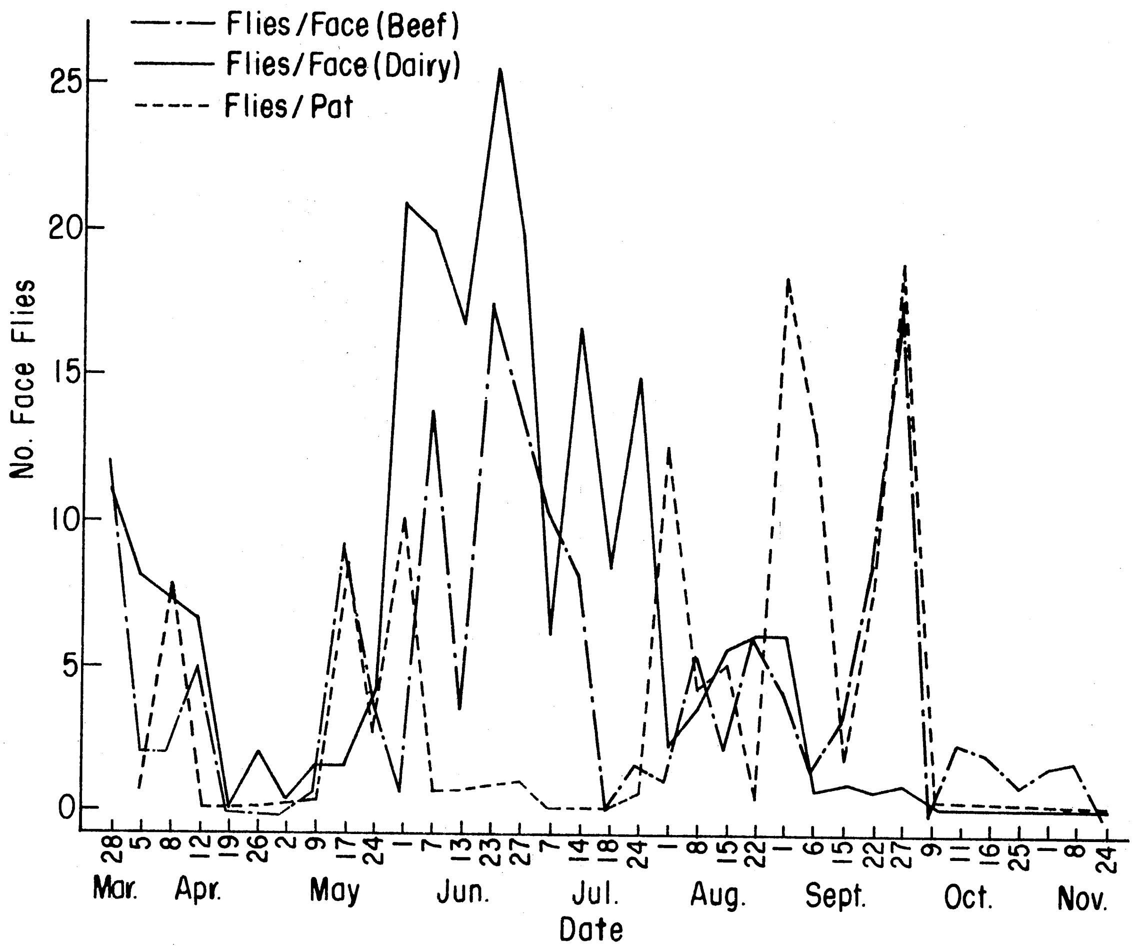

100
90
80
70
60
50
40
30
20
10
0
Percent Diapause
Jones
Oklahoma
North Dakota
16/8
15.5/8.5
15/9
14.25/9.75
14/10
Photoperiod (light/dark)

Figure 6. Population Levels of Face Flies During the 1978 Season in Osage County, Oklahoma.



Flies/Face (Beef)
Flies/Face (Dairy)
Flies/Pat
No. Face Flies
0
5
10
15
20
25
28 5 8 12 19 26 2 9 17 24 1 7 13 23 27 7 14 18 24 1 8 15 22 1 6 15 22 27 9 11 16 25 1 8 24
Mar.
Apr.
May
Jun.
Jul.
Aug.
Sept.
Oct.
Nov.
Date

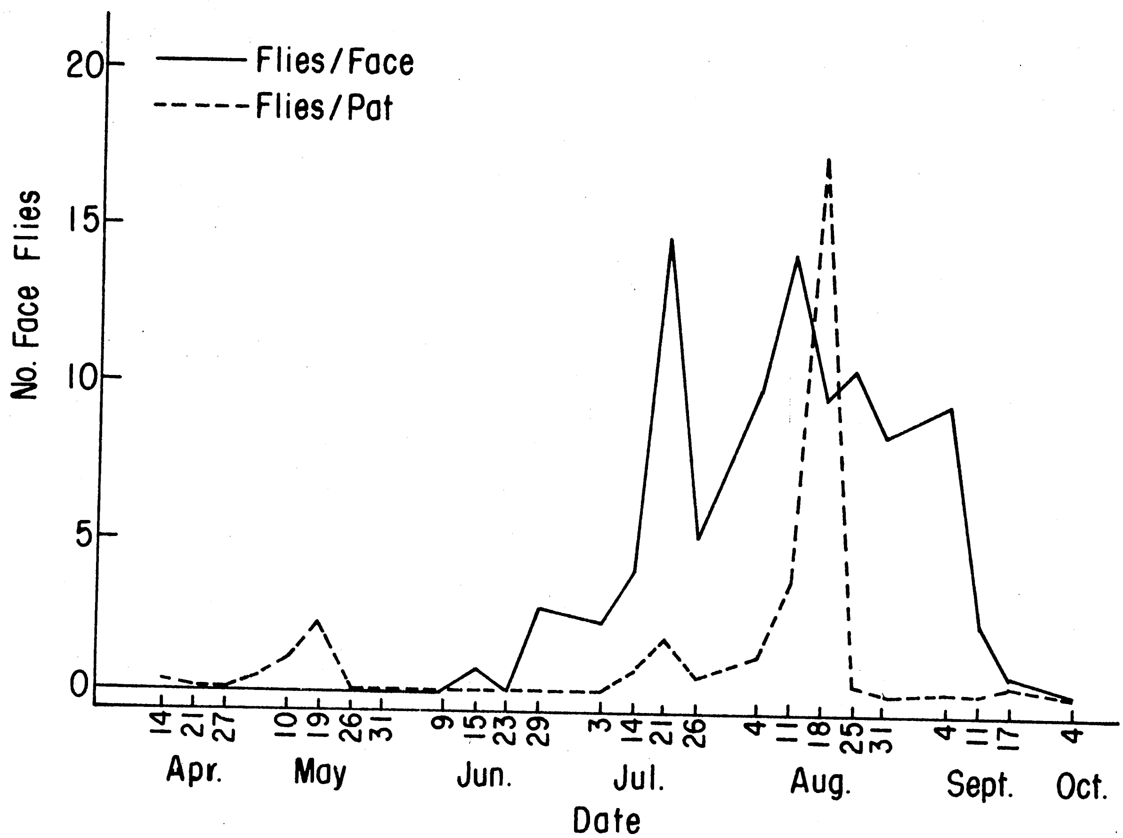
August 4 when it dropped sharply and did not rise above six flies/face for the rest of the observation period. The largest fly/pat ratios were September 17 and September 27 with 18.3 and 18.7 flies/pat, respectively. Smaller peak fly emergences from pats are shown in Figure 6. The number of flies/face declined from early April until the last of April. Few face flies were on cattle until the end of May when the new emerging population occurred.

Face flies were observed near overwintering sites on October 11 in Osage County. Flies were observed each week until November 1 when the first flies were seen entering overwintering sites. The last date overwintering sites were visited was November 24 and many flies had entered the sites and flies were not seen anywhere else in the area. Face flies collected from in and around the overwintering sites exhibited physiological characteristics which is indicative of diapause, that is fat body development, ovarian hypertrophy and lack of mating.

Box elder bugs, Leptocoris trivittatus Say, were observed in both the spring and fall entering and leaving the overwintering sites the face flies had selected. This was somewhat unexpected and perhaps can be used to locate other face fly sites, as both insects seem to prefer similar overwintering sites.

Observations of cattle in Mayes County were started on April 7, 1978 (Figure 7). Face flies were first observed on June 23. Prior to June 23 a dairy herd was used as the survey herd. Some difficulty was encountered with the survey and from June 23 to September 17 a cow-calf herd in an adjacent pasture was used for the remainder of the surveys. The highest fly/face ratio was recorded on July 21 and August 11 in Mayes County. These ratios were 14.6 and 14.0 flies/face,

Figure 7. Population Levels of Face Flies During the 1978 Season in Mayes County, Oklahoma.



Flies/Face
Flies/Pat
No. Face Flies
20
15
10
5
0
14 21 27
10 19 26 31
9 15 23 29
3 14 21 26
4 11 18 25 31
4 11 17
4
Apr.
May
Jun.
Jul.
Aug.
Sept.
Oct.
Date

respectively. After the beef herd was placed in a pasture that could be surveyed the pats were collected from the same area for the remainder of the study. The numbers of face flies emerging from the collected manure pats was also relatively low during the study. The highest fly/pat ratio was recorded on August 18 with 17.1 flies/pat (Figure 4).

Face flies were observed for only a very short time in Payne County. Flies were first recorded on May 9 and last seen on June 27. On June 15 the highest population was observed on cattle, 8.1 flies/face. No face flies were observed after June 27. The highest number of flies recorded as emerging from pats was 3.1 and 2.3 flies/pat on May 18 and June 23, respectively.

CHAPTER V

DISCUSSION

A major problem encountered in the statistical analysis of the data from these studies was the amount of variation between replications. This variation was probably due to the fact that only a part of the total population of face flies entered diapause. House (1966) stated that diapause is not a fixed species characteristic and in any natural population there are going to be some individuals with the potential for diapause and other individuals who lack this potential. Therefore, he concluded that diapause was an environmental adaptation that is acquired by natural selection. That this principle applies to face flies is indicated in this study since, with one exception, there never was 100% diapause induction at any photoperiod at constant temperature or in the fall simulation studies where temperature was varied. Even in natural conditions there was not 100% diapause until October 23, but because only living flies were examined, it is probable that any flies not in diapause at this date were dead and therefore only diapausing flies were sampled.

In the geographic study peak diapause was observed at 13/13 (Jones) and 14/10 (Oklahoma and North Dakota)(Figure 1) whereas in the natural (Figure 4) and simulation (Figure 5) peak diapause was observed at 15.5/8.5 and 14.25/9.75. Therefore, there seems to be a shift in the position of the critical photoperiod in the one temperature geographic study to the natural or simulated fall environment. Saunders (1976) noted that a constant temperature frequently modifies the degree of response or alters the position of the critical photoperiod. The difference of the percentage response exposed to the laboratory conditions (constant temperature) and those exposed to natural conditions indicated that the response may have been altered in the laboratory experiments where one temperature (no thermoperiod) was used.

The statistical analysis indicates that the number of days flies are exposed to a diapause inducing environment was important. Valder et al. (1969) stated that only in the first 24 hours post-ecdysis can adult face flies be stimulated to enter diapause and that any longer exposure only intensifies the physical characteristics of diapause. However, in these studies it was found that flies exposed for 14 days to diapause inducing conditions had a higher percentage in diapause than flies exposed to the same conditions for seven days (Tables I, II, and III). To determine if geographical strains of face flies responded differently to various diapause inducing conditions, flies were exposed for seven, nine, 11, and 14 days. Higher percentages of flies from all three colonies were in diapause when exposed to nine, 11, and 14 days as compared to the seven day exposure. However, exposure for longer than nine days did not significantly increase the percentage of flies in diapause.

Significantly more male face flies entered diapause than females at all temperature-photoperiod combinations tested ($P > .05$). This agrees with the reports of Caldwell and Wright (1978), Stoffolano and Matthysse (1967), and Valder et al. (1969). One possible explanation of this fact is that it is an adaptation of the face fly to insure enough males are available in the spring for mating as the adult female overwinters unmated.

In other insect species that have a large geographic range it has been found that the species sometimes will respond to the diapause inducing conditions differently in one part of its range than in another. Danilyevsky (1965) stated that a one hour decrease in critical photoperiod could be expected for each 3^{o} increase in latitude in the Lepidopteran, Acronycta. Tauber and Tauber (1972) found a one hour difference critical photoperiod between strains of Chrysopa carena and Depner and Harwood found a similar difference between strains of Anopheles freeborni. If such a difference has occurred in the face fly there should be a one hour difference between strains from the north and south. Face flies from North Dakota (northern) and Oklahoma (southern) responded in a similar fashion throughout the range of photoperiods used (Figures 1, 2, 4 and 5) with a critical photoperiod of 14/10. However, the colony of long term colonization (Jones) had a critical photoperiod of 13/11 thus showing that the long term colonization flies were not responding as flies in nature! There was no difference in the critical photoperiod inducing diapause in the two colonies from different geographic origins (Oklahoma and North Dakota). However, this has also been true in other insects. Ankersmit and Adkisson (1967) found no geographic variation in the Pink Bollworm, Pectinophora gossypiella. The range of latitude studied was 32^{o}N to 27^{o}S and critical day length was 12 to 13 hours in the entire range. One difference between the North Dakota and Oklahoma strains of face flies was that a higher percentage of Oklahoma flies entered diapause than North Dakota at all conditions tested. The reason for this seems unclear, but one possible explanation may be due to the much milder climate in the south. In the northern climate the temperature becomes the dominant factor much faster than in the southern climate. Flies that are responding slowly to the diapause inducing stimuli are killed by the low temperatures in the north, but in the south many would be able to complete diapause induction thus increasing the total number of flies entering diapause sites.

Beck (1977) and Saunders (1976) stated the photoperiod-thermoperiod combination generally determines the time of diapause, but that thermoperiod may be the more important of the two. In these studies diapause of the face fly was examined under three different conditions: constant temperature at four photoperiods shown in Figure 1, natural thermoperiod-photoperiod shown in Figure 4, and a simulation of natural conditions shown in Figure 5. In both studies where a thermoperiod was used a peak of diapause was at 15.5 hours, whereas in the constant temperature study the peak diapause was observed at 14/10 but no photoperiods of longer than 15/9 were used in the constant temperature studies. There was a peak of diapause at 14/10 in the natural and simulation that was higher than that of the constant temperature peak. However, all of these peaks are artificial, as in nature the flies never experience a photoperiod of 14 hours. They have either responded to conditions earlier in the fall or died. However, it is interesting to note that low percentages of diapause were observed at 15/9 in all three studies, whereas much higher percentages were observed at 15.5/8.5 and 14.25/9.75 when the thermoperiod is still somewhat similar in all three photoperiods. It then seems that it was photoperiod inducing the flies at 15.5/8.5 and 14.25/9.75 and not at 15/9. In nature, photoperiods shorter than 15/9 have thermoperiods with cold low temperatures that become important in determining the survival of the fly. After 15/9 it then seems that the thermoperiod may be more important than photoperiod due to the survival instincts of the species. These data agree with the results of Caldwell and Wright (1978) who state both photoperiod and thermoperiod are important. They don't agree with Beck (1977) and Saunders (1976) who say that thermoperiod is most important. In the case of the face fly it seems that thermoperiod does play an important role especially at low temperatures but that photoperiod is the overriding factor.

Danilevsky et al. (1970) states that ecologically speaking the threshold regions (the photoperiod that causes 50% of the individuals of a population to enter diapause) and the point at which 100% of a population is in diapause are most important. In the face fly in Oklahoma a photoperiod of 15.5/8.5 will stimulate 50% of the population to enter diapause. One-hundred percent of the population in diapause is probably never reached, but due to a sampling error it appears to be.

Masaki (1961) states that many times an introduced species will respond to the natural conditions as it can. I feel that this accounts for the lack of difference in critical photoperiod between the Oklahoma and North Dakota flies. It also accounts for the longer period of fly activity in Oklahoma as compared to that reported by Canada by Caldwell and Wright (1978) and Teskey (1969).

Conclusions

1. There was no geographic strain differences between Oklahoma

and North Dakota face flies in terms of critical photoperiod required to induce diapause.

2. Apparently more Oklahoma face flies entered diapause than North Dakota face flies under the conditions tested.

3. Both a thermoperiod and photoperiod are important in determining if an individual face fly will enter diapause but which is most dominant is yet unclear.

4. Face flies exposed to diapause inducing conditions responded in a more natural manner to a thermoperiod rather than constant temperatures.

5. Strain differences between colonies of face flies of long term and short term colonization are important and should be considered when selecting a colony for experimental work.

6. If information gained from experimentation is to be inferred back to a natural population, then utmost care should be taken to duplicate the natural conditions as closely as possible.

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APPENDIX

TABLES

TABLE VI

PERCENTAGE DIAPAUSE OF NORTH DAKOTA, OKLAHOMA, AND JONES FACE FLIES DIVIDED INTO SEX AT FOUR PHOTOPERIODS

Photoperiod	Colony	Number Dissected Each Sex	Percent Diapause Male	Percent Diapause Female
12	Oklahoma	50	46.0	38.8
	North Dakota	50	10.8	5.8
	Jones	50	11.5	4.0
13	Oklahoma	50	32.0	25.0
	North Dakota	50	31.8	21.5
	Jones	50	72.0	62.8
14	Oklahoma	50	61.0	49.0
	North Dakota	50	41.4	35.8
	Jones	50	32.5	15.0
15	Oklahoma	50	25.0	15.0
	North Dakota	50	12.3	11.3
	Jones	50	13.3	5.5

TABLE VII

PERCENTAGE DIAPAUSE OF NORTH DAKOTA, OKLAHOMA, AND JONES FACE FLIES AT 21°C AND FOUR PHOTOPERIODS

Photoperiod	Colony	Number Dissected Each Sex	Percent Diapause
12	Oklahoma	50	42.4
	North Dakota	50	8.2
	Jones	50	7.8
13	Oklahoma	50	28.8
	North Dakota	50	26.6
	Jones	50	67.4
14	Oklahoma	50	55.1
	North Dakota	50	38.6
	Jones	50	23.8
15	Oklahoma	50	20.2
	North Dakota	50	12.0
	Jones	50	9.4

VITA

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Master of Science

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