THE PREOVIPOSITIONAL PERIOD, OVIPOSITIONAL BEHAVIOR, AND MALE PREMATING ACTIVITIES FOR TABANUS ABACTOR PHILIP (DIPTERA: TABANIDAE)

By

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THE PREOVIPOSITIONAL PERIOD,

OVIPOSITIONAL BEHAVIOR, AND

MALE PREMATING ACTIVITIES

FOR <u>TABANUS</u> <u>ABACTOR</u>

PHILIP (DIPTERA:

TABANIDAE)

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CHAPTER I

INTRODUCTION

Tabanids (Tabanidae: Diptera) are important pests of man and livestock throughout the world (Chvala et al. 1972). Their aggressive and erratic feeding behaviors cause losses in livestock production due to general annoyance, irritation, considerable blood loss (Hollander and Wright 1980b), interruption of foraging (Steelman 1976) and the mechanical transmission of disease agents (Krinsky 1976).

Tabanids are vectors of several diseases of man and animals worldwide, caused by such organisms as filarial worms (loiasis, elaeophorosis), trypanosomes (sura, mal-de-caderas), rickettsia or rickettsia-like organisms (Q-fever, anaplasmosis), bacteria (tularemia, anthrax), and viruses (equine infectios anemia, vesicular stomatitis, hog cholera, California encephalitis) (Krinsky 1976).

It is commonly accepted that most horse fly and deer fly species have similar life histories and exhibit similar types of behavior patterns (Pechumen et al. 1983; Tidwell 1973). Females of most tabanid species engage in a series of activities and processes which include premating and mating behaviors, host seeking and blood-feeding, digestion of the blood meal and oogenesis, and behaviors associated

with oviposition, all of which may be repeated several times in a lifetime (Downes 1969; Detinova 1962). Females seek a blood meal after they have mated, and a single mating is sufficient for the female's entire reproductive life (Lane and Anderson 1982; Chvala et al. 1972; Wilson 1967). After mating, most female tabanids attack a variety of hosts seeking a blood meal which is required for the development of eggs. The males do not suck blood, but feed on plant juices and are sometimes found on flowers and foliage (Jones and Anthony 1964). After taking a blood meal the females digest it and develop eggs, and most species oviposit in aquatic or semiaquatic habitats, normally over water or situations which are suitable for larval development. The narrow cylindrical eggs, 1 to 3 mm long, are deposited commonly in masses of 100 to 1000 arranged in a single layer, as in most Chrysopsini, or in several layers (normally two), as in Tabanini. The incubation period is greatly influenced by environmental factors, but usually lasts from 5 to 7 days in midsummer. After hatching, the larvae drop to the surface of the water or soil and quickly burrow into the earth to begin feeding. Species of _Tabanus_ and _Hybomitra_ are predatory on many kinds of soil invertebrates, and are even cannibalistic on each other. _Chrysops_ larvae are believed to be vegetarians.

Males usually emerge slightly before the females, and males of many species exhibit premating behaviors which may include hovering periods prior to the appearance of females

and the onset of mating (Chvala et al. 1972). Both males and females frequently seek carbohydrate meals, often as nectar sugars or honeydew residues (Kniepert 1984).

Sixty-four tabanid species have been reported in Oklahoma (Wright et al. 1986), and several are very important pests on cattle from May through September (Wright et al. 1984). More than 20 species can be found in north central Oklahoma, where the most abundant pests of cattle include _Tabanus abactor_ Philip, _T. mularis_ Stone, _T. sulcifrons_ Macquart, _T. subsimilis_ Bellardi and _Hybomitra lasiophthalma_ (Macquart) (Wright et al. 1984). The combined effect of attacks by all species produces the greatest impact on cattle in June and July (Perich et al. 1986).

Direct losses in beef and milk production have been attributed to the irritation and annoyance caused by tabanids, resulting from the energy expended against attacking flies and the actual blood losses due to their bites. Bruce and Decker (1951) reported that tabanid attacks reduced weight gains of beef cattle by 9.07 to 13.06 kg (0.24-0.34 kg/animal/day) in a 38 day study. In north central Oklahoma, blood losses of 200 cc per day were estimated during June and July (Hollander and Wright 1980b). Cattle exposed to tabanid attacks gained less weight than protected animals, and were 13% less efficient in feed conversion (Perich et al. 1986).

There has been little success in developing control methods for tabanids. Applications of insecticides to

restricted areas have not been very effective, and applications over wide areas have been moderately effective and more dangerous to non-target organisms (Howell et al. 1949). There are no repellents that are effective against tabanid attacks for any length of time. Presley and Wright (1986) showed that a 1.0% permethrin pour-on formulation (150-200 ml/Hd) can kill 60% of tabanids for three weeks on cattle. However, after two weeks there was not adequate residue to provide satifsactory levels of control, and even though permethrin caused mortality up to four weeks, it never prevented flies from feeding and causing damages associated with blood feeding before they died.

Tabanus abactor is the most abundant and important tabanid pest of cattle because of its high populations during June and July (Wright et al. 1984; Cooksey and Wright 1987), its persistance in obtaining a large blood meal (Hollander and Wright 1980b), and the length of blood-seeking activity from midmorning until dark (Hollander and Wright 1980a). *Tabanus abactor* has also been shown to transmit the causative agent of anaplasmosis, *Anaplasma marginale* (Sanborn et al. 1932), while at least five other species in Oklahoma are also capable of vectoring the disease (Howell et al. 1941).

The preferred habitat for adult females of *T. abactor* is thought to be in timber-edge areas (Cooksey and Wright 1987). The continuous emergence of adults throughout the season produces an estimated population of over 500,000

host-seeking females per day in a 2.1 km^2 area during July (Cooksey 1985).

Female T. abactor prefer feeding on the legs or underline of cattle, and nearly triple their body weight upon taking a blood meal (Hollander and Wright 1980b). Blood-engorged females remain in the area where they take their blood meal and after ovipositing, many will take another blood meal within 72 to 96 hours (3 to 4 days) (Cooksey and Wright 1987). Using mark-recapture techniques, Cooksey and Wright (1987) found that 9.2 and 8.9% of engorged T. abactor were recaptured in 1982 and 1983 respectively, if cattle were not present in the area. The majority of recaptured females were trapped on the 3rd (46.4%) and 4th (18.4%) days after release in 1982, and 30.9 and 29.8%, respectively, in 1983. Wright (Unpublished data) found that when cattle were returned to the release site each day after flies were marked and released, 82% of all flies that were recaptured were collected at the release site. However, if cows were not returned to the area, 64.7 and 60.7% of recaptured flies from 1982 and 1983, respectively, were trapped at least 0.4 km from the release site, indicating that females quickly dispersed from the area after oviposition when suitable hosts were not present.

Tabanus abactor has never been directly observed ovipositing in the field under natural conditions. In the lab it has previously taken 7-9 days for flies to oviposit in containers, which is not supported by field observations.

Very little is known about female reproductive biology such as their activities while eggs are developing or during oviposition, the time period required for egg maturation, their oviposition sites, and other specific behaviors associated with oviposition. This study was undertaken in an attempt to elucidate some of these factors for *T. abactor*, in addition to studies of male hovering activities for species present in north central Oklahoma.

CHAPTER II

HOVERING CHARACTERISTICS OF SIX HORSE FLY SPECIES (DIPTERA: TABANIDAE) OBSERVED IN NORTH CENTRAL OKLAHOMA

Introduction

Tabanids can have a significant impact on cattle (Perich et al. 1986) and are very difficult to satisfactorily control with insecticides applied to animals (Presley and Wright 1986). To develop other control measures, searches continue into the biologies of horse flies to discover potential weaknesses in life history which may be exploited in a control program. As Catts and Olkowski (1972) stated, insect mating habits are often unique and restrictive enough that a control program could exploit such behavior patterns to allow insecticide applications to be more effective and specific.

Male horse flies and deer flies hover individually or in small groups at specific times in the morning or evening, and in a variety of locations as a mating or premating activity (Wilkerson et al. 1985). Tabanids have been reported hovering at various heights in open areas of salt marshes, in shafts of sunlight in the woods, along forest roads and paths or forest-meadow interfaces, over or next to

rivers, above forest canopies and at mountain summits (Bailey 1948b; Blickle 1955, 1959; Corbet and Haddow 1962; Leprince et al. 1983).

Conditions responsible for the hovering of males and flight patterns of females through hovering areas are unknown for most species (Wilkerson and Butler 1984). Both light intensity and a suitable ambient temperature are apparently necessary to initiate hovering, but in most cases factors causing the cessation of hovering are not known. Hovering generally does not occur on cloudy or rainy days (Corbet and Haddow 1962; Magnarelli 1985b).

The literature concerning characteristic hovering by males and its association with mating was first reviewed by Bailey (1948b) and since then by Downes (1969) and Wilkerson et al. (1985). Of over 3500 described species worldwide, Wilkerson et al. (1985) provide references to male swarming, hovering and mating behaviors for 58 species. This paper presents information of male hovering and mating activities of six Oklahoma tabanid species, including the first observations of hovering and mating of _T. abactor_.

Materials and Methods

Observations of male hovering activities were made from mid April to early August, 1987, at an Oklahoma State University rangeland area of Payne County, Oklahoma, dominated by Postoak-Blackjack Forest type vegetation interspersed with grasslands (Ewing et al. 1984).

Observations were made from before dawn to approximately 11:30 a.m. central daylight savings time (CDST), and in the evening from 7 p.m. to 9:30 p.m. Parameters such as time, temperature, wind velocity and wind direction were recorded during the observation periods. Representative individuals of all species observed hovering were captured with an insect net to insure positive identification.

Results and Discussion

Males of six species of horse flies were observed hovering in the study area, Hybomitra lasiophthalma (Macquart), Esenbeckia incisuralis (Say), Tabanus abactor Philip, T. calens L., T. equalis Hine and T. sulcifrons Macquart. Table I summarizes the characteristics or conditions associated with hovering for each species. Each species was found to be restricted in its hovering activities to definite sites and times.

Hybomitra lasiophthalma

Males were extremely numerous throughout the study area during late April, such that 5-10 males were observed at any one site, with sites just a few meters apart. They hovered at heights from 0.6-4 m, but were most common at 1.5-1.8 m; those hovering at 4 m were among the branches of an oak tree. Males hovered with their bodies parallel to the ground in direct sunlight and shade.

Males commonly started hovering at sunrise if

TABLE I

CHARACTERISTICS ASSOCIATED WITH MALE HOVERING BEHAVIOR FOR SIX HORSE FLY SPECIES IN OKLAHOMA

Species	Inclusive Dates for Hovering Observations*	Time of Day (CDST)	Observed Temperature Range (°C)	Duration of Hovering Period (Min)	Site	Usual Height
Hybomitra lasiophthalma	18 Apr-8 May (20)	7:00-8:30 a.m.	9.4-20.0	90 min	Forest openings	1.8 m
Tabanus equalis	29 Jun-3 Jul (3)	8:20-8:50 p.m.	24.4-26.1	30 min	Wooded areas	0.9 m
Esenbeckia incisuralis	13 Jun-28 Jun (8)	9:00-10:30 a.m.	23.3-31.1	90 min	Grassy clearings, west end	0.6 m
Tabanus abactor	8 May-5 Aug (30)	9:00-10:30 a.m.	23.3-31.1	90 min	Grassy clearings, east end	0.6 m
Tabanus sulcifrons	8 Jul-7 Aug (8)	6:50-7:15 a.m.	14.4-23.3	15 min	Above tree canopy	6-9 m
Tabanus calens	5 Aug-6 Aug (2)	8:20-8:40 p.m.	21.7-22.2	20 min	Over a road	0.6 m

*Numbers in parentheses represent number of days observations were made

temperatures reached 9.4°C by that time. On April 23, 1987, the beginning of the hovering period was delayed 75 minutes until the air temperature reached 9.4°C, after which males appeared and hovered normally for 1.5 hours.

The duration of the hovering period from the appearance of the first to the last male ranged from 1.5-2.25 hours. The period of greatest activity occurred for approximately 30 minutes, beginning shortly after the first male appeared. Temperatures at the end of the hovering period on different days ranged from 17.8-20.0°C and the latest time males were observed hovering was 9:30 a.m., at an air temperature of 18.9°C.

Magnarelli (1985b) reported that H. lasiophthalma in Connecticut hovered between 7:00 a.m. and 12 noon at temperatures of 17-30°C in forest clearings, and only in direct sunlight (3200-4800 foot-candles). They hovered at 0.25-2 m above the ground facing directly into or away from the sun with their bodies parallel to the ground. Leprince et al. (1983) reported H. lasiophthalma hovering above a 3-4 meter oak tree on a mountain summit in southwestern Quebec. Here it is reported that H. lasiophthalma hovered at a much lower temperature and ended earlier than reported by Magnarelli (1985b). Oklahoma specimens also oriented to and away from the sun but commonly faced many other directions.

Magnarelli (1985b) found no evidence of pair formation or mating during the hovering period. Five pair formations and two matings were observed during the hovering period in

1987. In each case, male flies pursued and captured females in flight and the pair flew to the ground to complete copulation.

Tabanus equalis

On three evenings from June 29 to July 3 ten to twenty males per evening were observed hovering in a 2-3 acre woodlot where the canopy was continuous overhead and where the vegetation was not very dense at ground level. Flies hovered under the canopy 0.9-1.2 m above the ground, between 8:20 and 8:50 p.m. at temperatures of 24.4-26.1°C. The only other report of T. equalis hovering was that by Wilkerson et al. (1985), which came from the label of a pinned specimen from Kansas, which was collected while hovering 0.9 m above the ground at dusk on June 24, 1964.

Esenbeckia incisuralis

Males frequently hovered in the morning hours from June 13-28 between approximately 9:00 and 10:30 a.m. They were always near the west side of grassy clearings, hovering in direct sunlight at a height of about 0.6 m with their bodies tilted at approximately a 40 degree angle, their heads positioned higher than their abdomens. Flies faced in all directions while hovering, and changed directions frequently when a breeze was present.

Wilkerson et al. (1985) reported that Esenbeckia incisuralis var. tinkhami Philip never hovered or formed

aggregations, but that males waited for females on flowers that both sexes used when nectar-feeding. Jones (1956), however, often observed both sexes hovering in the morning hours when they were actively feeding on brown-eyed susan wild flowers (Rudbeckia bicolor Nutt.). He also observed one mating at 9:00 a.m. on the ground among the flowers.

Tabanus abactor

Males of T. abactor were first observed hovering on May 5, 1987, about 2 weeks before females were routinely captured in CO_2 traps. Fifty hours of observations revealed that hovering males were abundant in certain areas throughout the study area. They usually hovered near the east ends of grassy clearings in and adjacent to wooded areas, with 5 to 10 males at each clearing during peak hovering periods.

Tabanus abactor hovered only on clear sunny days with very little or no wind; no flies hovered on overcast or rainy days. Males hovered in direct sunlight from 9:00-10:30 a.m., at a height of 0.3-0.6 m with its body tilted at a 30° angle (Figure 1). Hovering started at approximately 9:00 a.m., peaked between 9:00 and 10:00 a.m. and gradually declined between 10:30 and 11:00 a.m. The duration of the hovering period from the appearance of the first to last male on clear and warm days ranged from 45-120 minutes, with an average time of 80 minutes. Observations were always made on mornings when the temperature was above 23.3°C. The

Figure 1. Male *T. abactor* hovering at a height of 0.6 m at the east end of a grassy clearing.

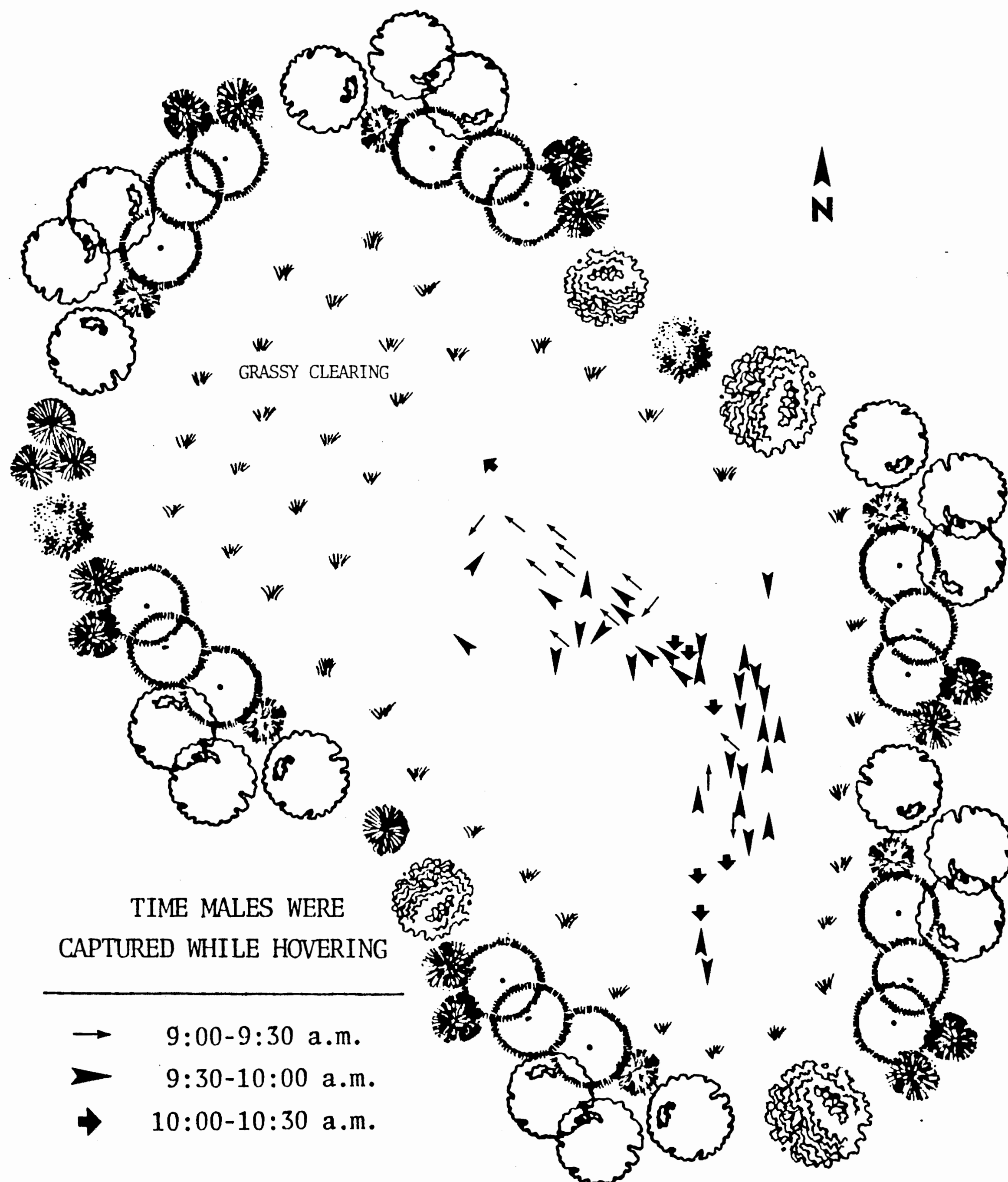
hovering period usually began at temperatures between 23.3 and 27.8°C and ended at temperatures between 26.7 and 31.1°C. The latest time males were observed hovering was at 11:02 a.m. at a temperature of 29.4°C.

Occasionally hovering males landed on neaby vegetation where they slowly walked up and down the stem with their bodies at varying angles toward the sun. Perhaps this behavior was to regulate body temperature.

Males were extremely numerous at one of the hovering sites on July 31, 1987, where a total of 50 flies were captured as they arrived from 9:15 to 10:30 a.m. There was a relationship between the time, location, and orientation of hovering males in the 19 x 29 m clearing as illustrated in Figure 2. Each arrow in the figure represents a specific place and direction males faced while hovering when they were captured. Early in the hovering period, between 9:00 and 9:30 a.m., 10 out of 13 males (77%) were present along the center toward the east side of the clearing, and faced northwest (lengthwise) along the clearing. Between 9:30 and 10:00 a.m. 20 out of 30 flies (67%) were captured along a north-south tree line at the east end of the clearing and faced either north or south. Between 10:00 and 10:30 a.m. six out of seven flies (86%) were captured near the east side facing south. The reason for changes in specific hovering points and orientation with time has not been determined.

Despite observations on over 300 hovering males only

Figure 2. Location and orientation of hovering _T. abactor_ in a clearing, at different times of the hovering period on July 31, 1987. Arrows point in the direction that individual males faced while hovering.


N
GRASSY CLEARING
TIME MALES WERE
CAPTURED WHILE HOVERING
9:00-9:30 a.m.
9:30-10:00 a.m.
10:00-10:30 a.m.

two matings were noted. In both instances males captured females in flight and the pair flew to nearby vegetation to copulate for approximately ten minutes.

Tabanus sulcifrons

Numerous male T. sulcifrons were observed hovering between 6-9 m above the treetops at dawn on four days between July 15 and July 28, 1987. Approximately five males per 25 m^2 began hovering about 20 minutes after daybreak, 5:51 a.m. on July 15 and 5:58 a.m. on July 28, and ended between 6:06 a.m. (July 15) and 6:13 a.m. (July 28). Similar observations were made on August 6, 7 and 8, and in all cases the duration of hovering was exactly 15 minutes. Temperatures at the beginning of the hovering periods ranged from 14.4 to 23.3°C and did not change greatly during the hovering period on a given day.

Tabanus sulcifrons had previously been reported to hover at tree-top levels 9 m above the ground, 20-30 min after daybreak at light intensities of 1-5 foot-candles, and at temperatures above 15.5°C in Ohio and Missouri (Hine 1903, 1906; Hasemann 1943).

Tabanus calens

Tabanus calens is not very abundant in north central Oklahoma, but four specimens were observed hovering at sunset, between 8:20 and 8:40 p.m. on August 5 and 6 over portions of a dirt road which ran north and south through

the study area. Flies hovered 0.6 m above the road in areas where oak tree branches extended about 4 m overhead, and faced south along the road. Temperatures at the beginning of the hovering period were 23.3 and 22.2°C, and at the end were 22.8 and 21.7°C respectively. The time and temperature at which *T. calens* hovered was similar to that reported by Haseman (1943) in Missouri and Hagman et al. (1948) in New Jersey.

There does not appear to be a direct correlation with the male hovering period of five blood-feeding species and the daily blood-seeking activity patterns of the respective females (Hollander and Wright 1980a). Males of *H. lasiophthalma* and possibly *T. sulcifrons* hovered at a time when the least number of blood-seeking females were active during the day. However, *T. equalis* and *T. calens* males hovered in the evening during the crepuscular period when blood-seeking females were the most active. Males of *T. abactor* hovered in mid-morning, at a time when some females are seeking a blood meal but before such activity peaks in the afternoon or evening. For those species with partial or extensive overlapping hovering and host-seeking periods, unmated females may have flight patterns or behaviors that allow the males to recognize and mate with them. Also, males may not respond to mated host-seeking females, or these females do not frequent hovering areas.

It is believed that matings associated with male

hovering are rarely seen because males move too fast to follow them when pursuing females (Wilkerson and Butler 1984). Corbet and Haddow (1962) reported that only two or three females of _T_. _thoracinus_ were seen while observing hovering males, and they witnessed no matings; however, by using a different sampling technique (a light trap) they demonstrated that females were in fact present and numerous at the hovering site (above the tree canopy) during the hovering period. Jones (1956) did not correlate observations of copulating _E_. _incisuralis_ with the occurrence of hovering activities, and Magnarelli (1985b) found no evidence of pair formation or mating for _H_. _lasiophthalma_. I saw only five _H_. _lasiophthalma_ pair formations and two matings during 40 hours of observations, and only two matings of _T_. _abactor_ during 50 hours of observations. These observations support the fact that mating is sometimes associated with hovering, but it is not known whether mating takes place at other times also. Additional studies of these and other species can help elucidate factors associated with hovering, and the relationship it has with mating activities.

CHAPTER III

DURATION OF THE PREOVIPOSITIONAL PERIOD FOLLOWING A BLOOD MEAL FOR *TABANUS ABACTOR* PHILIP (DIPTERA: TABANIDAE) IN NORTH CENTRAL OKLAHOMA

Introduction

Studies of the gonotrophic cycle for many hematophagous Diptera have been used to determine physiological age (Detinova 1968). Similar studies for tabanid species have been used to determine autogeny, seasonal parity, and rates of follicular development for many tabanid species (Magnarelli 1985a, 1976; Auroi 1982; Lane and Anderson 1982; Lake and Burger 1980; Magnarelli and Stoffolano 1980; Roberts 1980; Magnarelli and Anderson 1977, 1979, 1981; Thompson et al. 1979; Magnarelli and Pechumen 1975; Troubridge and Davies 1975; Thomas 1973, 1972; Wilson 1967).

Studies of the gonotrophic cycle can be used to determine blood-feeding and oviposition cycles, which are important in determining disease vector potential, population dynamics, and the species which are important pests. The duration of the gonotrophic cycle affects the number of times flies blood feed and oviposit, and

consequently the total number of eggs produced per female. The length of the gonotrophic cycle may be an important part of the reproductive biology of a species by influencing the frequency of their host-seeking behavior throughout the season.

Tabanus abactor is the most abundant species in north central Oklahoma (Wright et al. 1984), yet little is known about its reproductive biology or oviposition times and sites. Tabanus abactor imbibes a very large blood meal relative to its size and weight (Hollander and Wright 1980b) and requires only one complete meal to develop a batch of eggs (Ehrhardt 1981). Previous research on this anautogenous species using mark-recapture techniques has shown that the majority of nonengorged flies were recaptured seeking a blood meal on days 1 and 2 post-release, while 46.4 and 18.4% of engorged flies that were recaptured were collected in search of another blood meal on the 3rd and 4th days respectively after blood feeding in 1982, and 30.9 and 29.8% on days 3 and 4 respectively in 1983 (Cooksey and Wright 1987). The objective of this study was to determine the rate of oogenesis following a complete blood meal by T. abactor under natural field conditions and temperatures.

Materials and Methods

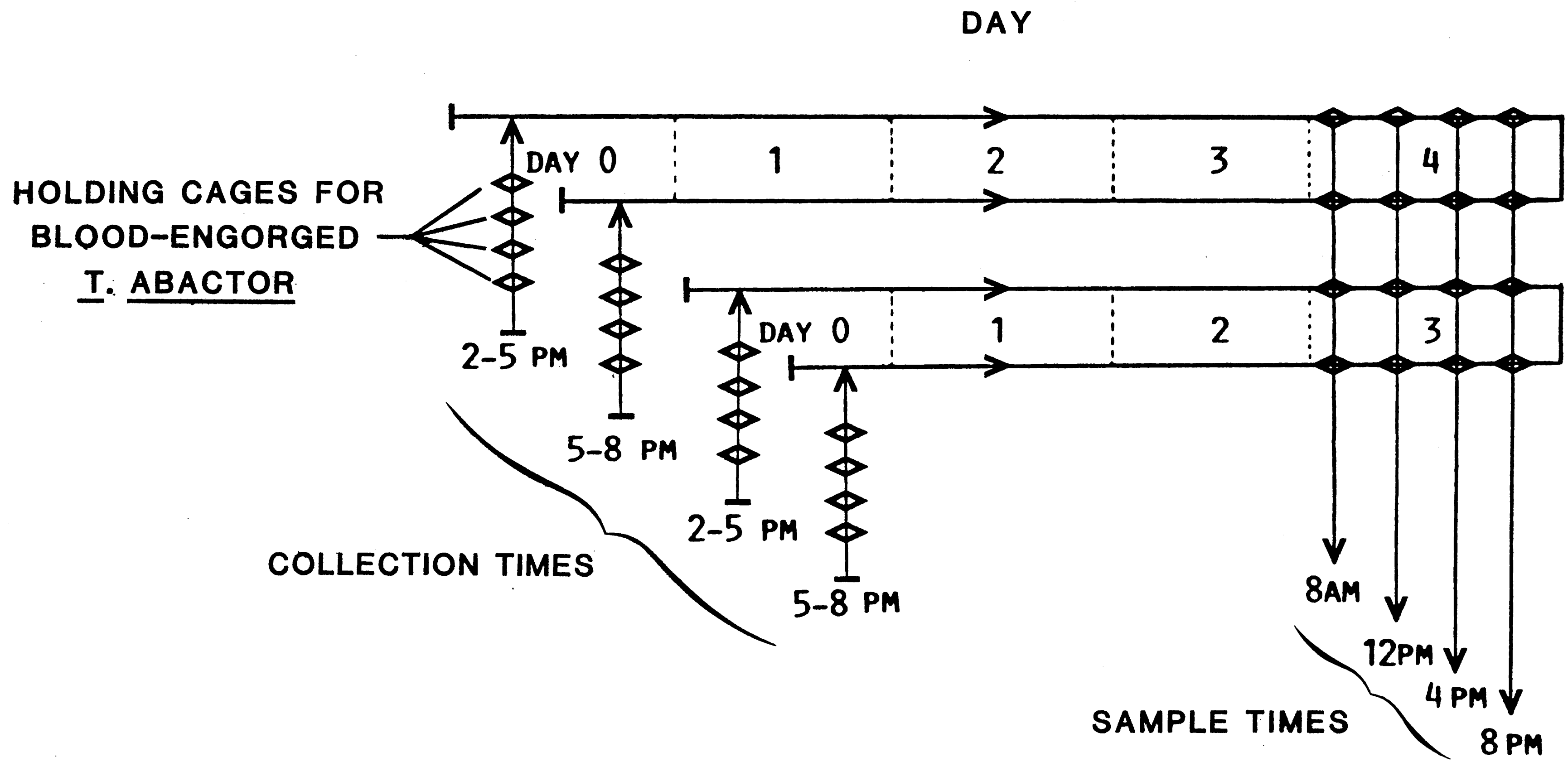
This study was done at an Oklahoma State University rangeland area located 11 km southwest of Stillwater in Payne County, Oklahoma. The area is dominated by Postoak-

Blackjack Forest type vegetation interspersed with grasslands (Ewing et al. 1984). Field trials were done from June to August of 1986 and 1987.

Engorged flies were collected from tethered cows with clear plastic cups using the technique described by Hollander and Wright (1980b) and Cooksey and Wright (1987). The engorged flies were collected during two periods, 2:00-5:00 p.m. and 5:00-8:00 p.m. central daylight savings time (CDST) on consecutive days (Figure 3), and flies from each period were randomnly placed in four individual cages. Thus, there were at least 16 sample cages from two consecutive collection days. An equal number of flies were placed in each cage per period, usually 50-60 if flies were abundant. All living flies in each cage were collected and immediately frozen at four sampling periods, 8:00 a.m., 12:00 p.m., 4:00 p.m., and 8:00 p.m. on the 3rd and 4th day after fully engorged specimens of a given trial were collected. The screened holding cages were 46 x 46 x 61 cm (0.28 m^3) with hanging vertical cloth strips added as resting sites and to prevent excessive flight activity. A 10% sucrose solution was provided in poultry waterers, and a sod clump and dried leaves taken at the collection site were placed on the floor of the cage to provide oviposition sites. Dried leaves included fallen oak leaves over a more compact layer of decaying oak leaves mixed with soil.

In 1986 caged flies were maintained in the study area on the ground in a shaded area, but in 1987 the cages were

Figure 3. Diagram of the experimental design used to sample previously engorged *T. abactor* at various times of the 3rd and 4th days after blood feeding.


DAY
HOLDING CAGES FOR
BLOOD-ENGORGED
T. ABACTOR
DAY 0
1
2
3
4
2-5 PM
5-8 PM
DAY 0
1
2
3
2-5 PM
5-8 PM
COLLECTION TIMES
8AM
12PM
4 PM
8 PM
SAMPLE TIMES

placed under a shelter constructed in this area to protect them from the sun and rain. Air temperature and relative humidity were continuously recorded with a hygrothermograph. In order to compare the rate of oogenesis under controlled temperatures, 16 cages of flies from two consecutive collection days were maintained in an insectary with a 16 hour photophase, at 30 ±1°C and 50-60% RH from July 27-31, 1987.

During each collection period all live flies were removed from the designated sample cages and placed on dry ice to stop subsequent ovarian development and oviposition. All specimens were stored at minus 51°C until the ovaries were examined under a microscope to determine parity using Polovodova's method (in Detinova 1962) and the stage of follicular development using the classification of Christophers (1911) as modified by Mer (1936). At least 10 ovarioles per ovary were examined.

Evaluations of follicular stages as described by Perich (1982) for _T_. _abactor_ during oogenesis were based on those of Clements (1963). The terminology used to describe the ovary and its parts is that used by Bertram (1962). Stages Ia through IIb are stages of oocyte development before the female seeks a blood meal and are not described here.

Stage IIIa: After a blood meal the follicle leaves the resting stage and yolk is deposited in the oocyte, which occupies about 50% of the follicle.

Stage IIIb: The follicle has increased in size and the

oocyte occupies two-thirds to three-quarters of the follicle.

Stage IVa: The follicle is larger and the oocyte occupies at least 90% of the follicle's length.

Stage IVb: The follicle becomes slightly deformed as it narrows and elongates to the length and shape of the mature oocyte. The chorion of the oocyte is very fragile and easily disrupted when the oocyte is removed from the ovary.

Stage V: The oocyte is mature and of maximum size, and is ready to be laid.

Sac Stage: After oviposition the tunica of the ovariole's pedicel is left as an expanded sac containing remnants of the follicular epithelium. This sac eventually contracts to form a more compact body called a follicular relic (or yellow body), which is present in the uniparous specimen at the base of the subsequent developing oocyte. After oviposition the remnants of the follicular epithelium from each oocyte apparently coalesce into a single large relic, which persists for the life of the female.

Results

During this study 7084 engorged flies were collected and placed in the holding cages, and 5405 were removed and dissected. There was no correlation between the time of the collection period when the flies engorged, ie. afternoon or evening, and oviposition on either the 3rd or 4th day. Ambient temperature during oogenesis regulated oogenesis and

therefore the time elapsed between engorgement and oviposition. Therefore the data were grouped according to mean ambient temperature over the respective time period allowed for oogenesis in order to examine temperature effects on the rate of oogenesis. The resulting temperature categories are listed in Table II, and include an average high and low daily temperature and an overall mean temperature for all days in each temperature category. The number of flies examined for each category is also included. The rate of oogenesis at six temperature categories with mean temperatures of 22.4, 23.3, 25.5, 27.4, 30.0 and 32.8°C were analysed. The temperature category 25.5°C included three trials at a mean temperature of 25.4°C and one trial at 25.6°C. Similarly, the temperature category 30.0°C included three trials at 30.2°C and one at 29.9°C.

Rates of follicular development and parity were dependent on temperature and increased with increasing temperatures except at the highest mean temperature of 32.8°C. The lowest rates of oogenesis and oviposition occurred at mean temperatures of 22.4°C and increased to a maximum at a mean temperature of 30.0°C. Specimens developing at a mean temperature of 32.8°C did not have as high oogenesis rates as those at 30.0°C, and had increased mortality. Tables III through VII present the data as the number of flies with ovarioles in a specific stage of development at times between 60 and 101 hours, 3 and 4 days after blood feeding. Figures 4 through 8 illustrate the

TABLE II

TRIALS GROUPED TOGETHER ACCORDING TO MEAN TEMPERATURE FOR 3 AND 4 DAY TRIALS IN 1986 AND 1987

Dates	Days in Trial	Number of Flies Dissected per Trial	Temperature (°C) Mean High	Mean Low	Overall Mean
7/14/87-7/17/87	3	355	27.9	16.8	22.4
6/29/87-7/3/87	4	298	26.9	19.7	23.3
6/30/86-7/3/86	3	460			
7/21/87-7/24/87	3	461	29.6	21.2	25.4
6/26/87-6/29/87	3	390			
7/20/87-7/24/87	4	376			
6/25/87-6/29/87	4	230	30.2	21.1	25.6
7/16/87-7/20/87	4	406			
7/7/87-7/10/87	3	491	31.4	23.4	27.4
7/3/86-7/7/86	4	426			
7/6/87-7/10/87	4	364	31.9	23.0	27.4
7/17/86-7/20/86	3	105			
7/23/86-7/26/86	3	270	34.2	26.1	30.2
7/28/87-7/31/87	3	289			
7/27/86-7/31/86	4	179	30.0	29.7	29.9
7/24/86-7/28/86	4	120			
7/28/86-8/1/86	4	72	40.8	24.9	32.8

percentages of follicular stage changes with time. No samples were taken between the last sample of day 3 at hour 76.5 and the first sample of day 4 at hour 85.5. During this nine hour night time period lower temperatures probably influenced oogenesis rates by slowing oocyte development.

Over 90% of all flies undergoing oogenesis at a mean temperature of 22.4 and 23.3°C had follicles in stages IIIb or IVa until after hour 85.5 (Table III and Figure 4). At this time the percentage of specimens with stage IVb follicles increased to 55% of 40 specimens by the last sample of the 4th day at hour 100.5. Specimens with follicles in stage V first appeared after hour 92.5 and increased to 12% of 40 specimens by the end of the day at hour 100.5. No specimens were parous by hour 76.5 or 100.5, indicating that no flies had oviposited by the end of day 3 or 4 at a mean temperature of 22.4 and 23.3°C respectively.

At a mean temperature of 25.5°C follicles progressed through stage IIIb and were in stage IVa by hour 61.5 (Table IV and Fig. 5). Seventy-nine percent of 138 specimens had developed follicles to stage IVb by hour 85.5. Slightly over 12% of the specimens collected at 72.5, 73.5 and 76.5 hours had follicles in stage V and there was little increase in development overnight as indicated by the 7.2 and 22% in stage V at the morning collection of 85.5 and 88.5 hours. Over 45% of 367 specimens collected at 89.5 to 93.5 hours, noon to 4:00 p.m. had follicles in stage V. At the last four collection times 93.5 to 100.5 hours at the end of day

TABLE III

NUMBER OF T. ABACTOR IN 5 STAGES OF FOLLICULAR DEVELOPMENT AT A MEAN TEMPERATURE OF 22.4°C FOR FLIES SAMPLED AT 61.5-76.5 HOURS AFTER ENGORGEMENT AND 23.3°C FOR FLIES SAMPLED AT 85.5-100.5 HOURS AFTER ENGORGEMENT

Hours After Feeding	Time of Collection	Number of Specimens in Developmental Stages					Total Number
		IIIb	IVa	IVb	V	Sac	
61.5	8 a.m.	-	22	1	-	-	23
64.5	8 a.m.	3	50	1	-	-	54
65.5	12 p.m.	6	23	-	-	-	29
68.5	12 p.m.	1	56	-	-	-	57
69.5	4 p.m.	5	36	-	-	-	41
72.5	4 p.m.	6	53	-	-	-	59
73.5	8 p.m.	-	32	3	-	-	35
76.5	8 p.m.	1	51	5	-	-	57
85.5	8 a.m.	1	25	1	-	-	27
86.5	8 a.m.	-	42	-	-	-	42
89.5	12 p.m.	-	31	4	-	-	35
92.5	12 p.m.	-	32	13	-	-	45
93.5	4 p.m.	1	18	8	3	-	30
96.5	4 p.m.	-	30	15	-	-	45
97.5	8 p.m.	-	16	15	2	-	33
100.5	8 p.m.	-	13	22	5	-	40

Figure 4. Rate of oogenesis for *T. abactor* measured by follicle stages present 61.5-100.5 hours after engorgement, at a mean temperature of 22.4°C for flies sampled at hours 61.5 to 76.5 and 23.3°C for flies collected at hours 85.5-100.5 hours.

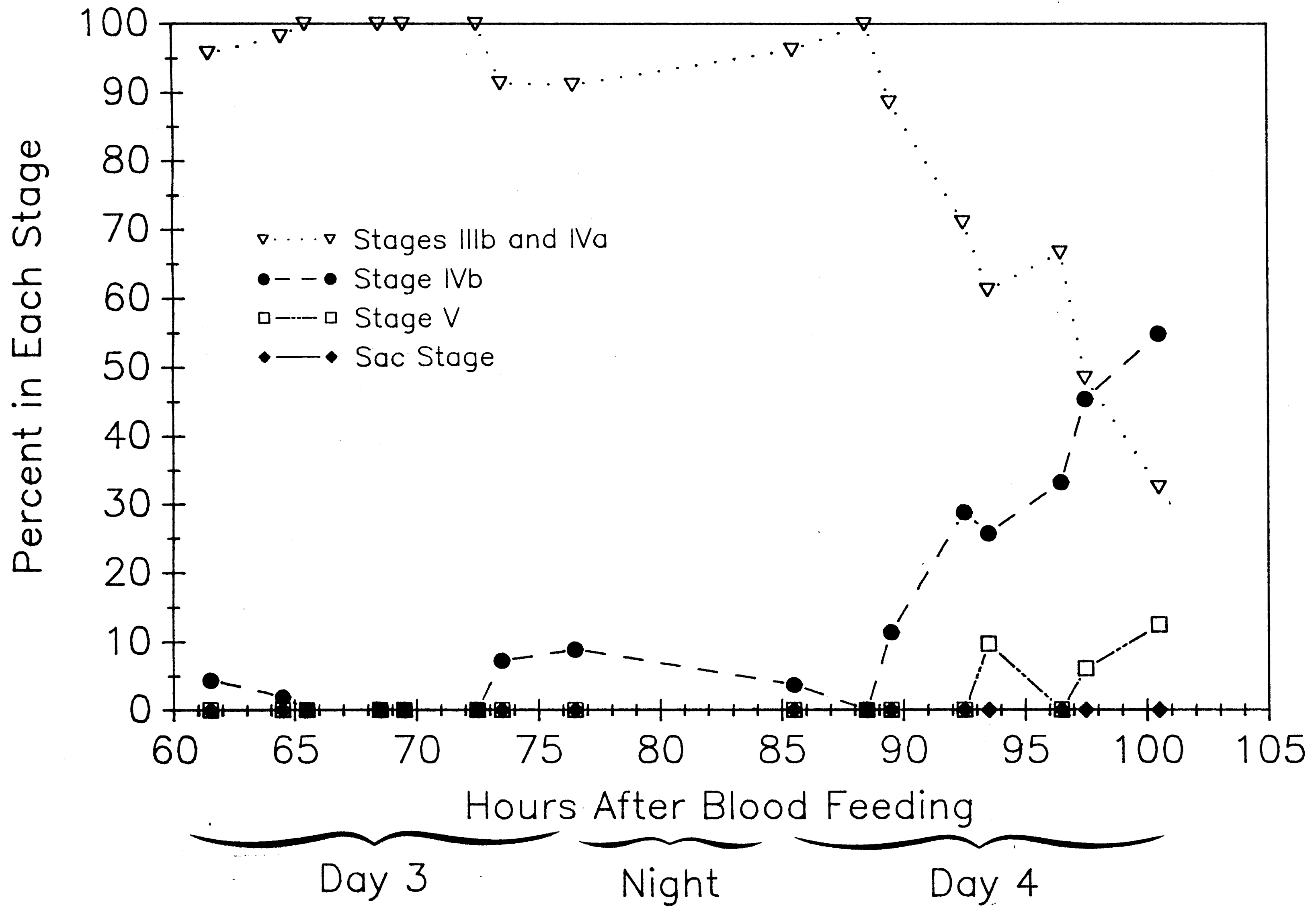
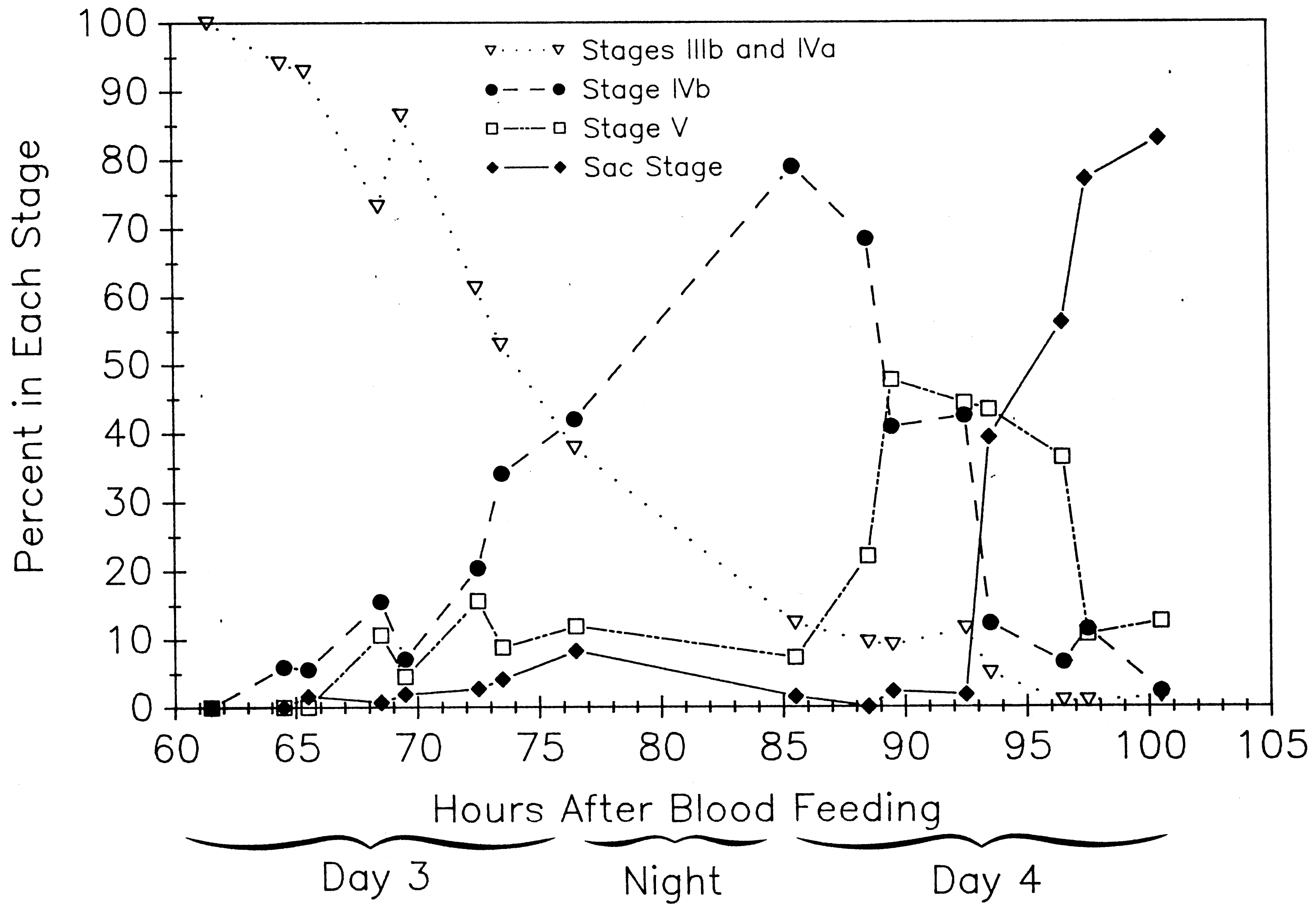

Percent in Each Stage
100
90
80
70
60
50
40
30
20
10
0
Stages IIIb and IVa
Stage IVb
Stage V
Sac Stage
60
65
70
75
80
85
90
95
100
105
Hours After Blood Feeding
Day 3
Night
Day 4

TABLE IV

NUMBER OF T. ABACTOR IN 5 STAGES OF FOLLICULAR DEVELOPMENT AT A MEAN TEMPERATURE OF 25.5°C WITH SPECIMENS SAMPLED AT 16 INTERVALS FROM 61.5 TO 100.5 HOURS AFTER ENGORGEMENT

Hours After Feeding	Time of Collection	Number of Specimens in Developmental Stages					Total Number
		IIIb	IVa	IVb	V	Sac	
61.5	8 a.m.	9	135	-	-	-	144
64.5	8 a.m.	5	139	9	-	-	153
65.5	12 p.m.	2	115	7	-	2	126
68.5	12 p.m.	-	104	22	15	1	142
69.5	4 p.m.	1	134	11	7	3	156
72.5	4 p.m.	-	114	38	29	5	186
73.5	8 p.m.	7	83	58	15	7	170
76.5	8 p.m.	2	71	81	23	16	193
85.5	8 a.m.	2	15	109	10	2	138
88.5	8 a.m.	-	12	87	28	-	127
89.5	12 p.m.	-	12	54	63	3	132
92.5	12 p.m.	1	12	48	50	2	113
93.5	4 p.m.	-	6	15	53	48	122
96.5	4 p.m.	-	1	8	44	68	121
97.5	8 p.m.	-	1	14	13	94	122
100.5	8 p.m.	-	2	4	17	112	135

Figure 5. Rate of oogenesis for *T. abactor* at 25.5°C measured by follicle stages present from 61.5 to 100.5 hours after engorgement.


Stages IIIb and IVa
Stage IVb
Stage V
Sac Stage
Percent in Each Stage
0
10
20
30
40
50
60
70
80
90
100
60
65
70
75
80
85
90
95
100
105
Hours After Blood Feeding
Day 3
Night
Day 4

4, 64% of 500 specimens had oviposited and 80% of those collected during the two 8 p.m. samples, hours 97.5 and 100.5, had oviposited, indicating that at this temperature 75-80% of the flies oviposit in the late afternoon or evening of the 4th day.

At 27.4°C (Table V and Fig. 6) almost all specimens had passed follicular stage IIIb and were in stage IVa when the first sample was taken on day 3 at hour 61.5. All specimens collected through 12:00 p.m., up to 68.5 hours, had follicles in stage IVa or IVb. By the last sample on day 3 at 76.5 hours, 12.6, 35.7, 17.9 and 35.8% of the follicles of 95 specimens were in stage IVa, IVb, V or sac stage respectively. However, by the next sample time at 8:00 a.m. the following morning (85.5 and 88.5 hours), 30.0 and 60.0% of the 200 specimens dissected had stage V follicles or had oviposited, respectively. These flies probably oviposited the previous evening. Only 40% of the flies sampled at 12:00 p.m. (92.5 hours), had oviposited. At the four subsequent sampling times at 4:00 and 8:00 p.m., 93.5-100.5 hours, 81-95% of the flies had oviposited. At 27.4°C, oogenesis had increased so that 84% of the specimens had oviposited by 4:00 p.m. and 92.5% by 8:00 p.m., respectively. Some of these had probably oviposited as early as the end of the 3rd day, 76.5 hours after blood feeding.

Oogenesis rates were greatest at a mean temperature of 30.0°C (Table VI and Fig. 7). By the end of the 3rd day at

TABLE V

NUMBER OF *T. ABACTOR* IN 5 STAGES OF FOLLICULAR DEVELOPMENT AT A MEAN TEMPERATURE OF 27.4°C WITH SPECIMENS SAMPLED AT 16 INTERVALS FROM 61.5 TO 100.5 HOURS AFTER ENGORGEMENT

Hours After Feeding	Time of Collection	Number of Specimens in Developmental Stages					Total Number
		IIIb	IVa	IVb	V	Sac	
61.5	8 a.m.	1	43	5	-	-	49
64.5	8 a.m.	-	30	23	-	-	53
65.5	12 p.m.	-	45	7	-	-	52
68.5	12 p.m.	-	25	35	-	-	60
69.5	4 p.m.	-	38	17	8	-	63
72.5	4 p.m.	-	21	15	25	2	63
73.5	8 p.m.	-	15	24	3	14	56
76.5	8 p.m.	-	12	32	17	34	95
85.5	8 a.m.	-	1	8	38	61	108
88.5	8 a.m.	2	3	6	22	59	92
89.5	12 p.m.	-	3	8	46	36	89
92.5	12 p.m.	-	-	-	28	60	88
93.5	4 p.m.	-	1	-	12	85	98
96.5	4 p.m.	-	-	-	19	82	101
97.5	8 p.m.	-	1	-	10	100	111
100.5	8 p.m.	-	-	-	5	98	103

Figure 6. Rate of oogenesis for *T. abactor* at 27.4°C measured by follicle stages present from 61.5 to 100.5 hours after engorgement.

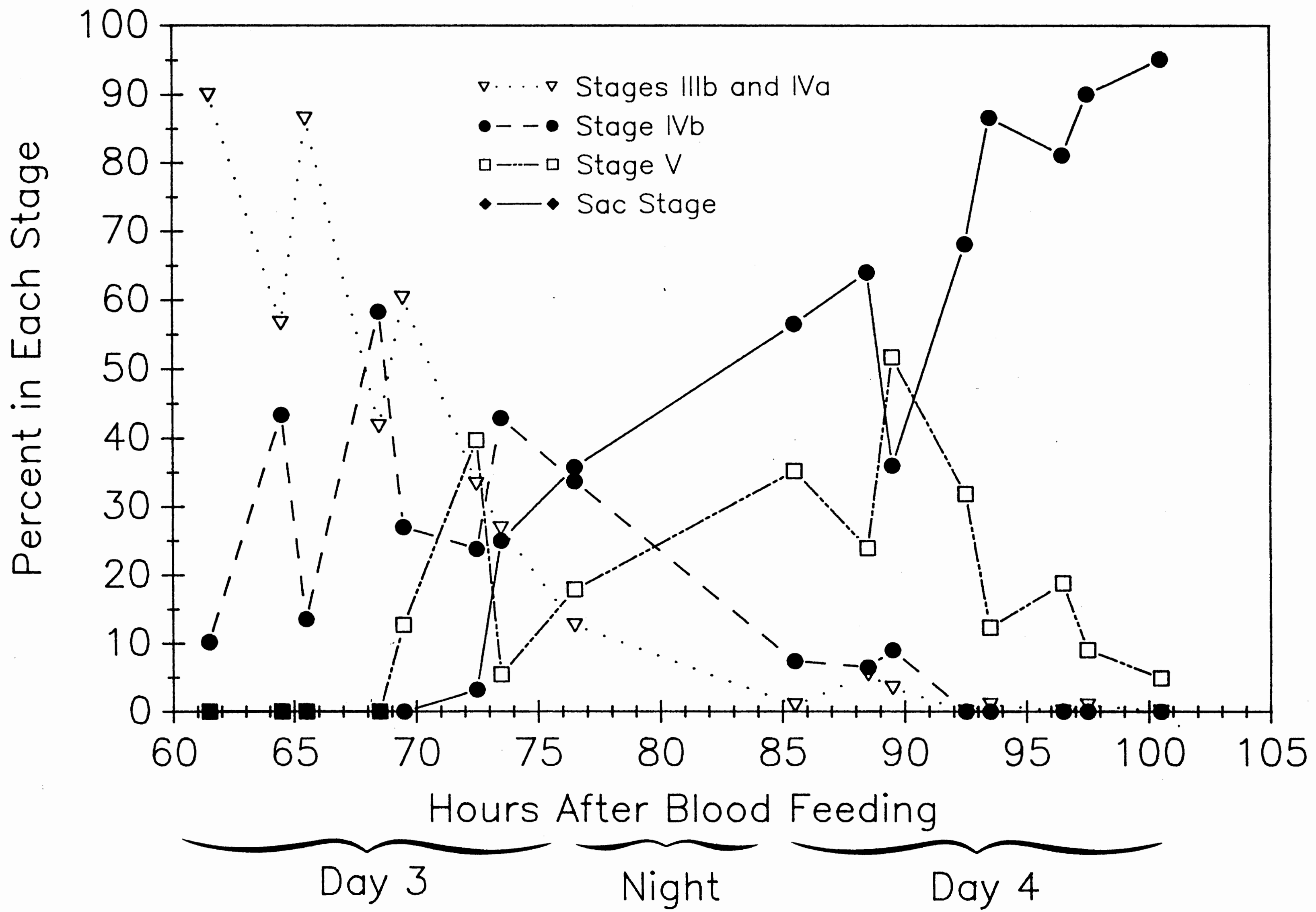
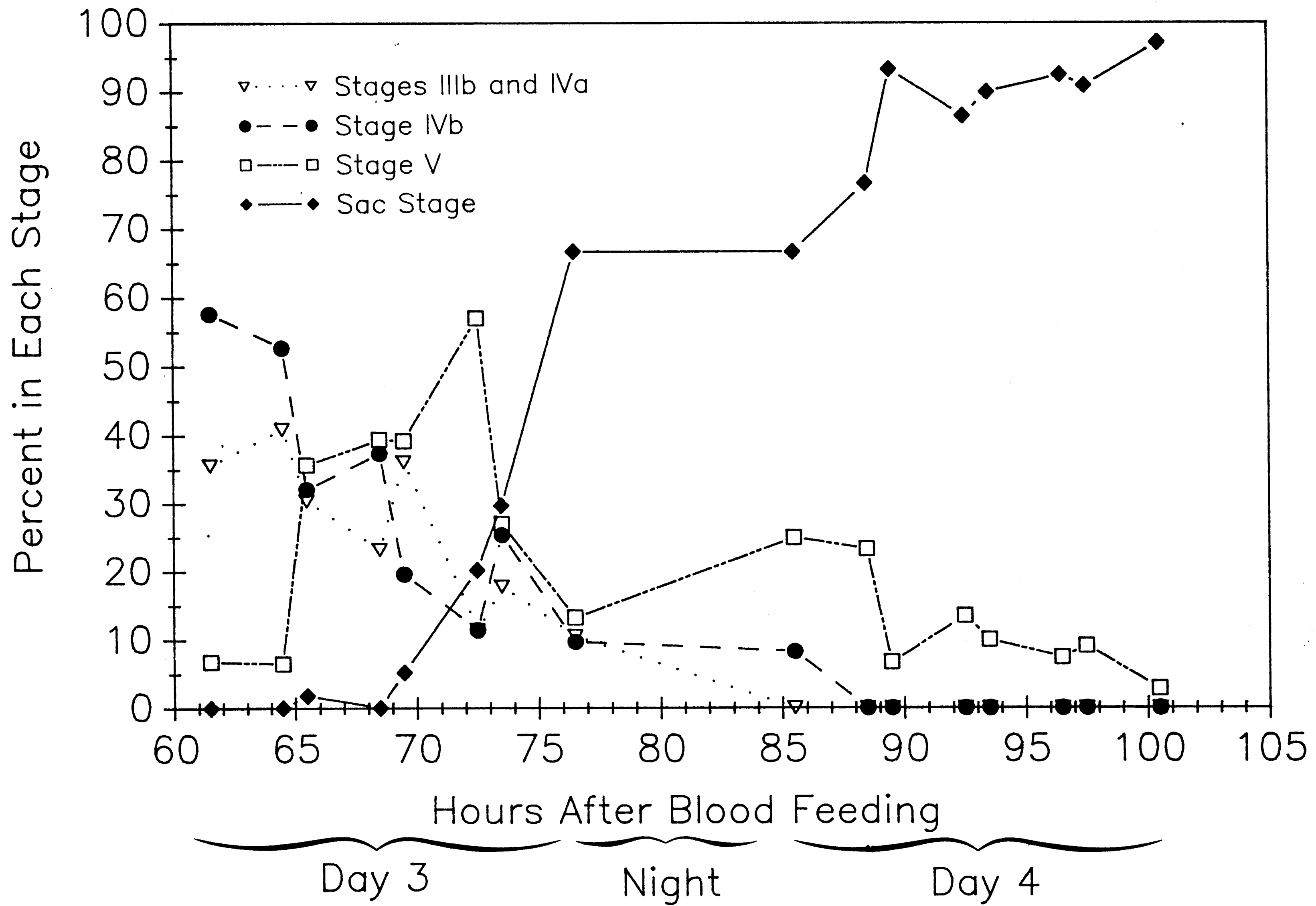

Stages IIIb and IVa
Stage IVb
Stage V
Sac Stage
Percent in Each Stage
Hours After Blood Feeding
0
10
20
30
40
50
60
70
80
90
100
60
65
70
75
80
85
90
95
100
105
Day 3
Night
Day 4

TABLE VI

NUMBER OF *T. ABACTOR* IN 5 STAGES OF FOLLICULAR DEVELOPMENT AT A MEAN TEMPERATURE OF 30.0°C WITH SPECIMENS SAMPLED AT 16 INTERVALS FROM 61.5 TO 100.5 HOURS AFTER ENGORGEMENT

Hours After Feeding	Time of Collection	Number of Specimens in Developmental Stages					Total Number
		IIIb	IVa	IVb	V	Sac	
61.5	8 a.m.	2	19	34	4	-	59
64.5	8 a.m.	4	34	49	6	-	93
65.5	12 p.m.	-	17	18	20	1	56
68.5	12 p.m.	5	18	37	39	-	99
69.5	4 p.m.	1	34	19	38	5	97
72.5	4 p.m.	1	12	13	65	23	114
73.5	8 p.m.	4	17	30	32	35	118
76.5	8 p.m.	1	11	11	15	76	114
85.5	8 a.m.	-	-	1	3	8	12
88.5	8 a.m.	-	-	-	7	23	30
89.5	12 p.m.	-	-	-	1	14	15
92.5	12 p.m.	-	-	-	5	32	37
93.5	4 p.m.	-	-	-	1	9	10
96.5	4 p.m.	-	-	-	2	25	27
97.5	8 p.m.	-	-	-	1	11	12
100.5	8 p.m.	-	-	-	1	35	36

Figure 7. Rate of oogenesis for *T. abactor* at 30.0°C measured by follicle stages present from 61.5 to 100.5 hours after engorgement.


Stages IIIb and IVa
Stage IVb
Stage V
Sac Stage
Percent in Each Stage
0
10
20
30
40
50
60
70
80
90
100
60
65
70
75
80
85
90
95
100
105
Hours After Blood Feeding
Day 3
Night
Day 4

8:00 p.m., 76.5 hours, 66.7% of 114 specimens had oviposited and by the following morning collection at 8:00 a.m., 73.8% of 42 specimens had oviposited. During the next six collection periods through 100.5 hours 92% of 137 specimens had oviposited; probably 2/3 to 3/4 of these had oviposited by the evening of the 3rd day 76.5 hours after engorgement. It is probable that 73-76 hours after engorgement at 30°C many specimens oviposit and immediately search for another blood meal.

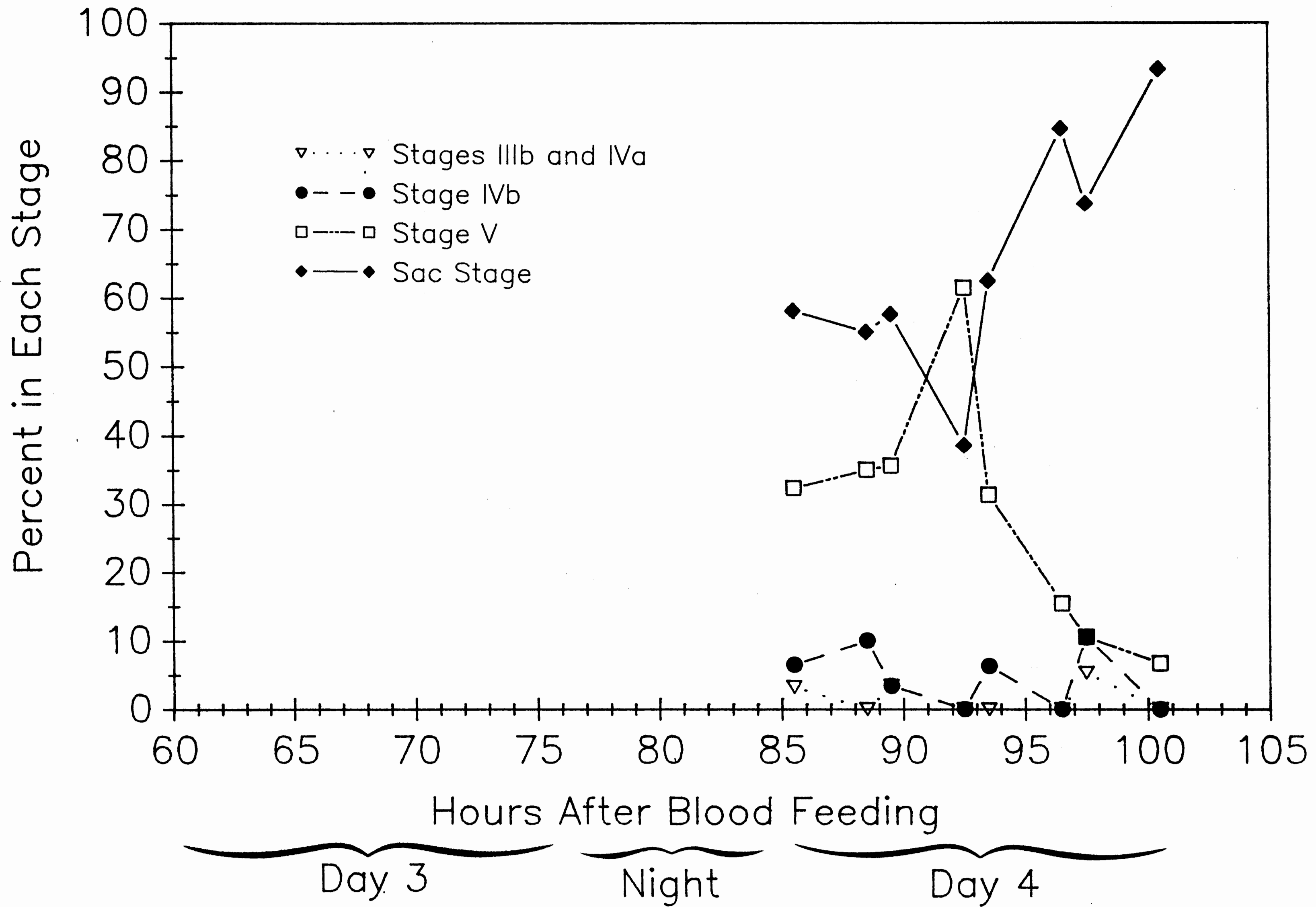
Flies that matured oocytes at a mean temperature of 32.8°C (Table VII and Fig. 8) were collected toward the end of a peak in the seasonal population of *T. abactor*, at a time during the summer which was characteristic of high temperature and low humidity and when flies may have been physiologically older. Only day 4 was sampled with the assumption that follicle changes occurred on day 3 similar to those at other temperatures. Specimens with follicles in stage IIIb, IVa and IVb were most abundant before the first sample at hour 85.5. Ninety-three percent of all specimens collected on day 4 were either parous or had follicles in stage V. Of 186 specimens, 30.1% had follicles in stage V and 62.9% were parous. Stage V specimens peaked at 61.5% of 13 specimens at hour 92.5, after which parity rates increased to 93% of 15 specimens by hour 100.5. The oogenesis and parity rate at 32.8°C was lower than at 30.0°C but possibly reflected the older population of flies or perhaps an impact of higher temperatures.

TABLE VII

NUMBER OF T. ABACTOR IN 5 STAGES OF FOLLICULAR DEVELOPMENT AT A MEAN TEMPERATURE OF 32.8°C WITH SPECIMENS SAMPLED AT 8 INTERVALS FROM 85.5 TO 100.5 HOURS AFTER ENGORGEMENT

Hours After Feeding	Time of Collection	Number of Soecimens in Developmental Stages					Total Number
		IIIb	IVa	IVb	V	Sac	
85.5	8 a.m.	-	1	2	10	18	31
88.5	8 a.m.	-	-	2	7	11	20
89.5	12 p.m.	-	2	2	21	34	59
92.5	12 p.m.	-	-	-	8	5	13
93.5	4 p.m.	-	-	1	5	10	16
96.5	4 p.m.	-	-	-	2	11	13
97.5	8 p.m.	1	-	2	2	14	19
100.5	8 p.m.	-	-	-	1	14	15

Figure 8. Rate of oogenesis for *T. abactor* at 32.8°C measured by follicle stages present from 85.5 to 100.5 hours after engorgement.


Percent in Each Stage
100
90
80
70
60
50
40
30
20
10
0
60
65
70
75
80
85
90
95
100
105
Hours After Blood Feeding
Day 3
Night
Day 4
Stages IIIb and IVa
Stage IVb
Stage V
Sac Stage

During the dissections the total number of ovarioles in both ovaries was counted for 51 specimens when follicles were in stage IV or V. There was an average of 80.95 developed follicles per ovary, or 161.90 (SE ± 5.74) per female.

Discussion

There are many intrinsic and extrinsic factors governing the rates of oogenesis for insects (Engelmann 1970), but temperature seems to be the most important for mated hematophagous flies after they have acquired a full blood meal. As Clements (1963) stated, oogenesis rates after a blood meal are controlled by temperature both indirectly by affecting the rate of digestion of the blood meal, and directly by affecting the rate of oocyte growth. Certain temperatures may affect different species differently, depending on temperatures they normally encounter in their natural environment throughout the season (Roberts 1980; Engelmann 1970). Laboratory studies that measured oogenesis rates for tabanids at a constant temperature may not have reflected oogenesis rates at seasonal ambient temperatures (Magnarelli 1985a; Auroi 1982; Magnarelli and Anderson 1979; Wilson 1967). Studies on mosquitoes have reported variations in the duration of the gonotrophic cycle as it relates to various temperatures and seasonal changes (Service 1968; Clements 1963).

This study allowed tabanids to remain subject to

natural environmental temperatures for their gonotrophic cycles by subjecting them to both daily temperature fluctuations and seasonal temperature ranges. The rates for oogenesis were positively correlated with temperatures, being highest at a mean temperature of 30.0°C and lowest at 22.4°C. If the mean temperature for the period of oogenesis was 25.5°C or above, at least 80-90% of all flies oviposited by the end of the 4th day, 100.5 hours after blood feeding. No flies oviposited by the end of day 4 at 23.3°C. At 25.5°C, 8.3% of 193 specimens oviposited by the end of day 3, and 83% of 135 specimens by the end of day 4. Most flies that oviposited at this temperature did so after hour 92.5. At 27.4°C, 36% of 95 specimens oviposited by the end of day 3, about 17 hours earlier than the similar increase in parity for flies at 25.5°C. By the end of day 4, 95% had oviposited. At 30.0°C, 18.4% more flies had stage V follicles on day 3 than at 27.4°C, and 67% of 114 specimens oviposited by the end of the day, 31% more than those that laid at 27.4°C. The temperature category 30.0°C had a group of flies held in an insectary under controlled conditions and showed very similar oogenesis rates as those seen in the field with a similar mean temperature. Rates of oogenesis for specimens at 32.8°C were similar to those at 27.4°C, but lower than those at 30.0°C, which may reflect inhibition due to unusually high daytime temperatures (mean = 40.8°C). Similarly, Roberts (1980) found that constant temperatures above 32.2°C caused lower than maximal oogenesis rates for 7

out of 11 tabanid species.

Significant increases in the number of specimens with follicles in the sac stage occurred in 8 p.m. samples on day 3, and in 4 and 8 p.m. samples on day 4. At 30.0°C high rates also occurred in 4 p.m. samples at hours 69.5 and 72.5. These increases in parity occurred 3-4 hours after each previous peak in specimens with stage V follicles, and represents the condition of follicles after oviposition has occurred. Therefore, for flies that ovipositied on day 3, oviposition occurred predominantly from hours 69.5-76.5 and on day 4 from hours 93.5-100.5. These times corresponded to samples taken at 8 p.m. of day 3, and 4 and 8 p.m. of day 4. The majority of oviposition therefore occurred after 12 p.m. of each of the 3rd and 4th day after blood feeding and continued until the end of the day.

Cooksey and Wright (1987) reported that 46.4 and 30.9% in 1982 and 1983, respectively, of previously engorged _T. abactor_ were captured seeking another blood meal on day 3. According to their mark-recapture methods, these flies were recaptured at 24-hour intervals at 10:00 a.m. of each day and included a collection for day 3 between 86-91 (mean = 88.5) hours after engorgement. This sample corresponded to the first sample of day 4 of the present study. At temperatures of 27.4°C or above in the present study, 57-67% of all flies had oviposited by hour 88.5, representing a potential 10-35% increase over previous field results using mark-recapture techniques. It is believed, however, that

since previous results were an average for each summer's work, a range of temperatures were represented and included those below 27.4°C, which would increase the time needed for oogenesis and subsequent oviposition. It is also believed that the majority of flies collected at the 10:00 a.m. sample of day 4, which represented flies collected on day 3, were actually captured in search of a blood meal toward the end of the 3rd day, 72-76 hours after engorgement. This is supported by unpublished data (Wright) in which a substantial number of previously engorged flies returned to cows on the 3rd day, 72-76 hours after engorgement. The results of each study, therefore, support the contention that flies seek another blood meal shortly after oviposition, even if oviposition occurs on the 3rd day after engorgement.

Temperature-affected oogenesis rates as seen here reflect what occurs at different times of the season, ie. early in the season at lower temperatures and later at higher temperatures, and behaviors associated with the gonotrophic cycle are in turn likely to be affected. It is important therefore to understand that results obtained in lab studies may be different than what occurs throughout the season for a particular species.

Ehrhardt (1981) and Cooksey and Wright (1987) reported that 1.3-3.4% of marked engorged flies were recaptured in search of a blood meal on and before the second day after release. It was assumed that these flies had not taken a

blood meal or had only taken an incomplete meal and returned for more blood. It is believed that hematophagous flies which do not acquire a sufficient amount of blood to develop all eggs will begin oogenesis in all primary oocytes, but a certain number will degenerate and be resorbed in response to insufficient nutrients (Bell and Bohm 1975; Detinova 1962; Woke et al. 1956). Such oosorption in Aedes aegypti mosquitoes is thought to begin 8-12 hrs after a blood meal, but may also occur in oocytes through stage IIIb, up to 30 hrs after a blood meal (Briegel 1985; Clements and Boocock 1984). Clements and Boocock (1984) reported that the majority of follicles which degenerated did so in stages IIIa and IIIb. In the present study 1.42% of all flies dissected had oocytes either in the ovarian diapause condition or undergoing resorption. Magnarelli (1983) noted that upon dissection of certain mosquito species, those follicles which resorbed oocytes were filled with much more debris than those which would have formed by the contraction of distensions after oviposition. This was most often seen in the present study between stages IIIa and IVa. Flies with follicles that appeared as such were not used to represent developmental rates, and a cut-off point based on observations of significant delays in development by day 3, was set at stage IIIa. Stages less developed than IIIb by day 3 or 4 represented unfed flies and were also excluded from the analysis.

Perich et al. (1985) examined 60 ovaries with ovarioles

in stage IIb and found that there were an average of 107 ovarioles per ovary. In the present study there were only 82 oocytes per ovary which matured to stage V. This is preliminary evidence to support the belief that similar to mosquitoes, _T_. _abactor_ may not demonstrate an "all or none" response in the number of oocytes that mature per ovary per blood meal, but depend on intrinsic factors operating after the blood meal is taken as oocytes begin to mature. This is an area which needs additional research.

CHAPTER IV

OVIPOSITIONAL SITE AND BEHAVIOR FOR *TABANUS ABACTOR* PHILIP (DIPTERA: TABANIDAE) IN NORTH CENTRAL OKLAHOMA

Introduction

The egg laying habits of the family Tabanidae are extremely variable (Cameron 1926), and are unknown for most of the economically important species (Jones and Anthony 1964).

Females usually place their egg masses on vegetation above or close to water, or near some other suitable larval habitat (Tidwell 1973; Khan 1953). The eggs are commonly glued together in masses consisting of a single layer for most *Chrysops* species, or two or more layers for most *Tabanus* and *Hybomitra* species (Pechuman et al. 1983; Tidwell 1973; Chvala et al. 1972). The eggs are white when laid but darken after a few hours (Sofield and Gaugler 1984; Pechuman et al. 1983).

Tabanus abactor Philip is the most abundant tabanid species in north central Oklahoma (Wright et al. 1984) but little is known relative to the ovipositional behavior or ovipositional sites of this species. Cooksey and Wright (1987) reported that most previously blood-fed females seek

another blood meal within 3 or 4 days, and as the last chapter indicated most females developed eggs and oviposited within this 3-4 day time period. The only report of T. abactor oviposition was that caged females laid their eggs in a double tiered very loose mass or scattered them on the bottom of the cage (Schomberg 1955). However, T. abactor has never been observed ovipositing under natural conditions. Observations of ovipositional sites, behaviors and the physical appearance of laid eggs for T. abactor in field cages are reported here.

Materials and Methods

This study was done in an Oklahoma State University Rangeland area of Payne County, Oklahoma. Observations of ovipositional sites, ovipositing females and laid eggs for T. abactor were made in conjunction with a study to determine the duration of the preovipositional period following a blood meal as described in Chapter 2 of this thesis. Engorged flies were collected from tethered cows with clear plastic cups using the technique described by Hollander and Wright (1980b) and Cooksey and Wright (1987). The engorged flies were collected during two periods, 2:00-5:00 p.m. and 5:00-8:00 p.m. central daylight savings time (CDST) on consecutive days, and flies from each period were randomnly placed in four individual cages. Thus, there were at least 16 sample cages from two consecutive collection days. An equal number of flies were placed in each cage per

period, usually 50-60 if flies were abundant. All living flies in each cage were sampled and immediately frozen at four sampling periods, 8:00 a.m., 12:00 p.m., 4:00 p.m., and 8:00 p.m. on the 3rd and 4th day after blood-engorged specimens of a given trial were collected. The screened holding cages were 46 x 46 x 61 cm (0.28 m^3) with hanging vertical cloth strips added as resting sites and to prevent excessive flight activity. A 10% sucrose solution was provided in poultry waterers, and a sod clump and leaf litter taken at the collection site were placed on the floor of the cage to provide oviposition sites. The leaf litter included a loose layer of fallen, dried oak leaves over a more compact layer of decaying leaves mixed with soil.

In 1986 caged flies were maintained in the study area on the ground in a shaded area, but in 1987 the cages were placed under a shelter constructed in this area to protect them from the sun and rain. Air temperature and relative humidity were continuously recorded with a hygrothermograph. A large Saran™ screen cage (6.1x8.5x2.5 m) was also built over undisturbed vegetation to provide as many natural ovipositional sites as possible, and jars of 10% sucrose solutions were provided here as well. In 1986, 655 flies were placed in the large cage from July 21-25, and 566 from July 22-28, and 109 and 184 specimens, respectively, were collected for dissection. Observations were made on the 3rd and 4th days when flies were removed from cages at 8 a.m., 12 p.m, 4 p.m. and 8 p.m. Parity determinations were made

when flies were dissected.

Results

Unlike reports of oviposition for most tabanids, _T. abactor_ oviposited on the ground or the covered floor of the cages. Eggs were found in the small cages below the surface of leaf litter (Figure 9) or on the floor of the cage beneath the sod clump when females could move easily beneath it. Eggs in the large cages were found on the ground beneath the leaf litter. No eggs or ovipositing females were ever seen above the surface of the leaf litter, either on the cage or anywhere in small trees. Sometimes females were observed to move backwards and place their abdomens within openings of leaf debris, and eggs were later found in these openings.

Females laid their eggs beneath leaves or sod clumps in the cages and were easily disturbed when exposed. Therefore, it was difficult to directly observe uninterrupted oviposition, from beginning to end. Some females, however, were observed as they continued to lay a few eggs after being disturbed and before they discontinued laying. As most of each egg protruded from the abdomen, the female attached the distal end to the substrate or another egg and lifted the abdomen to free the egg. Eggs were laid in loose piles, with individual eggs often randomly oriented with respect to the substrate or one another, which is in contrast to the ordered and compact masses characteristic of

Figure 9. Eggs of _T._ _abactor_ found in loose piles under leaf litter on the bottom of a holding cage.

many tabanid species. Eggs were white when freshly laid, but turned a darker gray after a few hours. After drying, the eggs which were laid in piles fell apart when touched or moved and thus were usually found scattered in a loose pile at the oviposition site.

Generally, oviposition occurred throughout the 3rd and 4th days after blood feeding, and peaked from mid afternoon to early evening. Freshly deposited eggs, along with ovipositing females, were most often seen at samples taken at 4 and 8 p.m. on the 3rd and 4th days. Parity rates of dissected flies were also highest at these times. Daily high temperatures occurred between 2 and 6 p.m. as reported in Chapter 2, and were correlated with times of oviposition.

Discussion

The ovipositional site and behavior associated with oviposition for T. abactor are unique with respect to the positioning and physical appearance of egg masses characteristic of other tabanids. There may be many physical or chemical stimuli involved in oviposition site selection by tabanids, but they are unknown for most species (Sofield and Gaugler 1984; Graham and Stoffolano 1983).

Workers who have held tabanids in cages or containers observed results typical for the family under natural field conditions (Magnarelli 1985a; Graham and Stoffolano 1983; Magnarelli and Stoffolano 1980; Jones and Anthony 1964). In these studies, all females oviposited on vertical or

horizontal areas of the cage which is similar to the ovipositional sites on vertical or horizontal parts of plants and other objects over or near water in nature. Although caged conditions used in the study were not identical to natural field conditions, the ovipositional sites and behaviors remained consistent in small and large cages and from year to year. Because ovipositional sites and behaviors of T. abactor were very similar in either small or large cages, it is believed that this species oviposits on the ground under leaf litter in the field as they did in the cages.

Endogenous circadian rhythms for ovipositional activity are common in insects (Saunders 1982) and mosquitoes have an ovipositional periodicity strongly influenced by light-dark changes (Chadee and Corbet 1987; Panicker et al. 1981; Clements 1963; Gillet et al. 1962). Ovipositional periodicity for tabanids is important as it influences subsequent host-seeking behaviors (Auroi 1982; Duke 1960). Many tabanid species commonly oviposit throughout the day, with a peak in ovipositional activity in mid afternoon (Graham and Stoffolano 1983; Sofield and Gaugler 1984; Bailey 1948a; Khan 1953). Graham and Stoffolano (1983) stated that it was at this time that average daily air temperature and light intensity were highest and relative humidity lowest. Tabanus abactor was also found to oviposit from mid afternoon to early evening during times of high temperature and low humidity. A similar type of strategy

was observed for the California coastal horse fly, *Apatolestes actites* Philip and Steffan, which oviposits in subterranean burrows of amphipods or isopods to protect the eggs from rapid dessication in a dry environment (Lane and Anderson 1983). Oviposition in places thought to be characteristic for *T. abactor* during the hottest parts of the day would insure that those sites chosen by females are the most protected from extremes of heat and dessication, and might provide a safer place away from free-roaming predators.

Larval habitats have been characterized by Chvala et al. (1972) into approximately four groups, including hydrophilic (aquatic), semihydrophilic (semiaquatic), edaphic (in drier soil far from water) and xerophilic (very dry) types. Ovipositional behaviors for species which develop in such habitats would therefore probably occur in or near such places. It is believed that the preferred larval habitat for *T. abactor* is in dry, well drained mineral soils of uplands (Schomberg and Howell 1955; Sanders, unpublished data; Wright, unpublished). This report of ovipositional activity and ovipositional sites suggests that the larval habitat for *T. abactor* in north central Oklahoma is well drained soil in post-oak blackjack woodlands.

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VITA 2

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