THE STABLE FLY, STOMOXYS CALCITRANS (LINNAEUS): BIOLOGY AND BEHAVIOR STUDIES

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PREFACE

The stable fly, Stomoxys calcitrans (Linnaeus) was recognized as an insect of veterinary and medical importance by Bouche as early as 1834. Yet, the biology and habits of this pest species are still incompletely known, even though it is a very common laboratory reared species used to evaluate potential toxicants or repellents. The author was responsible for one such evaluation program at the United States Department of Agriculture, Entomology Research Division, Insects Affecting Man and Animals Laboratory, Kerrville, Texas, and, during the course of routine experiments, became interested in investigating certain aspects of the biology and behavior of this interesting insect.

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INTRODUCTION

Stomoxys calcitrans (Linnaeus) is one of, if not the most widely distributed species of blood feeding Diptera affecting man and animals. For all practical purposes it is cosmopolitan, having been reported from all land areas except the polar regions. However, it is most abundant in temperate climatic zones such as the United States and Argentina. Furthermore, within these temperate regions the numbers of individuals is highly variable depending on local environmental conditions. Serious outbreaks have often been associated with specific agricultural practices, malpractices, or the natural accumulation of decaying organic matter.

The world-wide distribution has, no doubt, been partially responsible for the numerous common names ascribed to this insect from time to time. Currently, much of the world literature, including that of the Entomological Society of America, recognizes the common name to be "stable fly", even though the name does not well describe the habitat or any characteristics of the species. In addition, it is or has been called the "dog fly" in Florida and other gulf coast states, the "cattle fly" and the "biting fly" in New Zealand, and the "biting house fly", "stock fly", "wild fly", "beach fly", "straw fly", and "power mower fly" at other scattered locations.

Although the stable fly apparently does have feeding preferences when provided a choice, it can subsist and prosper on the blood of any of a large number of warm-blooded animals including man. Perhaps the

insect's choice of a host is dictated by the amount of protection afforded by the hair coat or habits of a prospective host. Among the domestic animals horses, cattle, hogs, dogs, cats, sheep, and goats appear to be subject to attack in about the order named.

The stable fly is a pest of considerable economic importance both in its depradations on livestock and as it affects the recreation of man. It has been accused of mechanical transmission of several livestock diseases, of reducing vitality of animals by taking quantities of blood, of distressing the animals so as to interfere with normal feeding, of causing reduced milk production in dairy cattle, and of causing such discomfort in man that he avoids affected recreational areas. The United States Department of Agriculture has estimated the dollar loss to the producer due to stable fly attack on cattle and calves alone to be $142 million annually. Perhaps a more graphic way to represent this loss is to recognize that the 74 million pounds of meat represented would provide the average annual beef ration for 740,000 persons.

In spite of its common occurrence and the serious economic losses attributed to the stable fly, control of this species is still generally unsatisfactory. As is often the case in entomology, one of the serious deficiences is the lack of information concerning the biology and behavior of the offending species. Thus, the purpose of the present investigation is to provide additional biological data about the stable fly that might be useful in development of control measures or concepts.

REVIEW OF THE LITERATURE

Problem and Economic Importance

Stomoxys calcitrans (Linnaeus) is a "biting" or blood feeding dipteran parasite of domestic animals and man that, because of its feeding activity, may contribute to the debility of a host by: (1) irritation during or in attempting the feeding act, (2) loss of blood, or (3) transmission of disease. DeFoliarts' (1963) observation that "the stable fly is probably the most underrated member of the fly complex on cattle" is, no doubt, a true assessment of the existing fly problem as it affects cattle, especially dairy cattle. However, as the hungry adult fly does not discriminate in its feeding, horses, man, pigs, and other animals are subject to attack. Pigs especially are tormented by stable fly attack when flies are numerous. The pigs commonly attempt to elude attack by entering wallows or hiding in buildings. Cattle and horses are attacked principally on the legs and get little rest or opportunity to feed, but constantly stamp their feet and otherwise fight the attackers (Bishop, 1913; Hearle, 1938; Knipling and McDuffie, 1956).

Although the most important role of the stable fly is considered to be that of an annoyer of animals and man, this fly has been either suspect or shown to be capable of transmitting a number of diseases. Bishop (1913, 1920) listed surra, souma, anthrax, and infectious anemia as transmittable by stable flies, as well as, recalling that the flies

act as an intermediate host for a species of roundworm which infests cattle. Sanders (1933) succeeded in transmitting anaplasmosis with stable flies and Ferris et al. (1955) were able to transmit the virus of vesicular stomatitis under experimental conditions for 1 to 3 days after infection of the flies.

Cases of myiasis involving stable fly larvae are quite rare but Onorato (1922) described a human intestional infection in which the larvae were regurgitated and reared out to adults. Porter (1924) reported extracting a larva from the foot of a boy. The only animal infection on record was described by Knipling and Rainwater (1937) from wounds in an unspecified domestic animal. Recently, in a personal communication, Knipling indicated he had reason to doubt the source of the larvae.

Many investigators have conducted milk production or weight gain studies on cattle, comparing production with and without fly control or describing the losses in production or monies due to a severe stable fly infestation. Bishop (1913, 1913a, 1920 (1926)) reported milk production decreases as a result of a severe outbreak in Texas during 1912 to be as much as 40 to 60 percent. Also in northern Texas alone over 300 head of cattle, mules, and horses, were killed directly or indirectly as a result of the fly attack. Freeborn et al. (1925), working in California, reported that during one month's confinement in a heavy infestation of stable flies, the milk production of 4 test animals decreased 9.26%. The studies of Bruce and Decker (1947, 1958) demonstrated very significant correlations between stable fly abundance and reductions in milk and butterfat production during the summer months of May through September. On the basis of two distinct regression lines,

average monthly rates of loss were established as 0.65 and 0.7% per fly per cow. They also present evidence that indicates depressed production continues for weeks beyond the end of the fly season. Granett and Hansens (1956, 1957) conducted fly control studies in New Jersey with methoxychlor sprays and dusts and found that the increase in milk production as a result of their treatments was more than enough to pay for the cost of fly protection.

Weight gain experiments by Cheng (1958) indicated that as a result of fly control treatments, the mean gain in weight of the treated group of cattle over the untreated group was 1/2 to 2/3 of a pound per animal per day. Similar data was obtained by Cutkomp and Harvey (1958) in Minnesota when fly control was applied by means of a treadle sprayer to beef animals on pasture. On the other hand, many investigators have reported negative data, usually because of environmental circumstances beyond their control. For example, Todd (1964) working in New Zealand was unable to correlate weight gains or milk production with the number of flies, but his work did suggest a possible correlation with variable weather.

The United States Department of Agriculture (1965) has estimated that for the years 1951-60 stable flies caused an average annual loss to cattle growers of $74,000,000 due to loss of animal weight and $68,000,000 due to loss of milk.

Nomenclature

In 1965 two catalogs were published that included the genealogy of Stomoxys calcitrans (Linnaeus). Both were written by H. C. Huckett (1965, 1965a), although one appears as a section in the United States Department of Agriculture publication entitled: "A Catalog of the

Diptera of America North of Mexico". The nomenclature and its synonymy as presented by Huckett are as follows:

Family: MUSCIDAE
Subfamily: STOMOXYINAE
Genus: STOMOXYS Geoffroy

Stomoxys Geoffroy, 1762. Hist. Ins., 2:538. Type-species

Conops calcitrans Linnaeus

Conops calcitrans. Linnaeus. Systema Naturae, 1758.

Empis calcitrans Scopoli, Entomologia carniolia, 1763.

Stomoxys calcitrans Fabricius. Systema entomologiae, 1775.

Stomoxys parasita Fabricius. Entomologia systematica, 1794.

Stomoxys inimica Robineau-Desvoidy. Essai Myodaires, 1830.

Stomoxys dira Robineau-Desvoidy. Essai Myodaires, 1830.

Stomoxys cybira Walker. List Diptera Insects British Museum, 1849.

Stomoxys occidentis Walker. Diptera. Vol. 1, 1852.

Recognition

Probably the most common statement one finds in the literature offered as a description of the stable fly is that "stable flies look like house flies and are of a similar size but have a slender, rigid, piercing and sucking proboscis projecting forward from beneath the head." (Bishop, 1913, 1920(1926); Dicke, 1958; Eddy, 1952; Hearle, 1938; James, 1947; Knipling and McDuffie, 1956; Todd, 1960; United States Department of Agriculture, 1941, 1953). Hearle (1938) and Todd (1963) both added the information that stable flies were grey or brownish-grey in color, and 4 dark longitudinal stripes on the thorax, and the abdomen was marked with several large, rounded, dark spots that resulted in a checkered appearance.

The original technical description is to be found in Systema Naturae (1758) but Malloch (1932) provided a detailed list of what he termed, "the most reliable recognition characters of the species". Malloch's paper is probably the most available source of a full technical description and interested persons are directed to it for details of the subfamily and genus as well as the species. The frontispiece of the present paper illustrates the characters in a 10X dorsal view of a female stable fly.

Larvae have been described by Newstead (1906), Bishop (1920(1926)), and Tao (1927) as typical, yellow-white muscoid larvae measuring about 4/5 inch in length at maturity. The large tail end is marked with two dark-colored buttons, each having three spiracular slits, and the body tapers to a sharp-pointed head.

Newstead (1906) and Bishop (1920(1926)) also characterized the pupa as a barrel-shaped, reddish-brown, one-fourth inch long chitenized enclosure that is slightly narrowed in front and broadly rounded behind.

Distribution and Abundance

Several literature references speak of the distribution of Stomoxys calcitrans as cosmopolitan or almost universal and comment on its close association with man and/or his agricultural practices (Bishop, 1913, 1913a, 1920(1926)); King, 1936; James, 1947). James (1947) enumerated 117 countries from all land areas of the world, except the polar regions, from which the stable fly has been identified.

In Europe, particularly Scandinavia, Stomoxys has received considerable attention. As early as 1844, Zetterstedt reported the fly to be common all over Scandinavia and Thomsen (1938) wrote that the stable fly often was a more common insect than the house fly in barns of

Northern Europe. Wilhelmi (1917) identified flies collected from barns on the German island of Riems as nearly all stable flies. In more recent years, Sømme (1958, 1959) has conducted extensive population counts of flies resting in Norwegian barns and has shown that stable flies make up a large part of the fly population during the summer months. Of 5954 flies observed in one count series in 11 barns, 74.5% were stable flies, 15.3% house flies, and 10.2% Fannia species.

In Britain, Mellor (1914) surveyed 5 typical village and rural situations during the summer of 1916 and reported finding one or more Stomoxys in each. Although not as abundant as Musca domestica, it was, at least, as well distributed.

In Africa, Roubaud (1911) found Stomoxys commonly along rivers in dry parts of the continent. Parr (1959, 1962) reported large numbers of flies in Uganda, East Africa only where bananas were grown or where cattle bomas were poorly maintained. In both cases, larval media was available due to poor agricultural practices and provided the only source of flies in the area.

In India, Chandhuri (1965) reported Stomoxys to be a severe pest in many localized areas, and Perrajic and Tirumalarao (1956) traced a serious infestation of flies to the use of cake manure on melons.

Kuwayama (1947) studied the seasonal prevalence of stable flies in Hokkaido and found adults active from approximately July 1-November 30, with the greatest numbers in August and September.

In New Zealand, recent changes in certain agricultural practices apparently favor abundant stable fly numbers during the warm months of January-June. Todd (1960, 1964) reported the fly had increased so sharply in recent years, especially in the North Island, that it had

become an urgent problem. The larvae production was traced to uncovered ensilage stacks where larvae counts up to 20,000/sq yd were recorded. Griffiths (1962) confirmed the observations of Todd.

Hearle (1938) named British Columbia and the Central Provinces as the areas of greatest Stomoxys abundance in Canada and explained that the flies preference for rotting vegetation as a breeding place naturally placed them in the major grain-growing and mixed farming areas of the Dominion.

In the United States many observations and investigations on the abundance of Stomoxys have been reported. With the exception of the Florida and East Coast "dog fly" problem, the reports trace the unusual outbreaks to poor agricultural or processing practices or the accumulation of decaying organic matter by urban dwellers. Thus, the abundance of the species appears to be dependent largely upon local and seasonal conditions.

Bishop (1913, 1913a, 1920(1926)) delineated the problem in the southern part of the country as a pest of more or less importance throughout the year, but usually most abundant in the latter part of the summer and during the fall. He felt that in the north and west the fly seldom became numerous enough to annoy stock until early fall. During Bishop's years of observation, several severe outbreaks occurred in the Mid-West and Texas and the source of each was traced to the straw stacks associated with harvesting grain. Under modern methods of harvesting, this source is almost non-existent as mobile harvesting equipment disperses straw in a thin layer throughout the field.

In 1941, the United States Department of Agriculture published a stable fly cicular that indicated the grain belt from north Texas to

North Dakota and the coastal area of Florida from Pensacola to Carrabelle to be the greatest problem areas in the United States. A second leaflet of the Department (1953) stated that the stable fly was found in all parts of the United States, but was especially numerous in the central and south-eastern states and in irrigated sections. Simmons and Dove (1941) reported on severe winter outbreaks in Florida and Georgia that originated from piles of peanut vine litter left in the fields. They estimated each pile was capable of producing 100,000 stable flies. Another extremely serious stable fly and house fly problem in the Sarasota, Florida area was investigated by Simmons and Dove (1942) and found to be associated with waste celery disposal from celery striping plants. The waste stripings were dumped and allowed to decay in piles in open fields. The authors calculated that this excellent larval medium contained up to 54,462 larvae/cu ft 18 days after the celery was dumped.

Another major recurring Stomoxys problem is related to the marine grasses and seaweeds that are cast upon the Gulf and Atlantic Coasts, especially in Florida. King and Lenert (1936) first reported finding stable fly larvae in "foul" seaweed along the Gulf Coast of Florida where adults were numerous and also found that adults had dispersed 15-25 miles inland from the larval sources. Simmons and Dove (1941, 1941a) further investigated abundance of Stomoxys along the northwest Florida coast and indicated August to October as the fly and seaweed months. Quarterman et al. (1951), while attempting to control the "dog fly" with DDT, found breeding in seaweed a common occurrence along the Florida Gulf Coast. Observations by Hansens (1956) in New Jersey indicated that a large part of the flies in barns can be stable flies and

that this species deposits its eggs in seaweed on the shore of New Jersey.

Schoof et al. (1954) found grass clippings to be the most common larval medium for stable flies in urban areas of Charleston, West Virginia, but also recovered larvae from fowl manure, garbage cans, and sea food wastes during fly abundance studies. Caked, wet grass clippings lodged under a power mower were found to contain Stomoxys larvae by Ware (1966).

Abundance on farms is obviously quite variable and as Hansens (1963) suggests: "is important locally where there is suitable breeding conditions". He reported a case in New Jersey where the problem was essentially confined to a barnyard wherein animals were fed chopped hay or silage. In Iowa, Dahm and Raun (1955) found there were periods when more than half the flies were thought to be stable flies; whereas in Wyoming, DeFoliart (1956) found only 3% to 4% of the flies in barns to be stable flies even in the height of the fly season. In 1956, Raun and Casey reported stable fly populations on cattle sometimes reached several hundred flies per animal in July and August. Guyer et al. (1956) found silage to be an important source of fly abundance in Michigan, especially productive were trench silos containing oats and peas.

In California, Anderson (1964) and Anderson and Poorbaugh (1964) found large numbers of Stomoxys larvae in poultry manure and adults in caged layer houses, but all the adult flies tested had consumed bovine blood. Thus it appeared that poultry ranches served as a source of flies, but the flies dispersed to obtain a blood meal elsewhere before returning to lay eggs.

Life History

Approximately 125 years ago Bouche (1843) discovered the larvae of Stomoxys calcitrans in animal manure that had been removed from a stable. From that time until the life history studies of Newstead (1906) in England, additional information on this insect was wanting. However, Newstead traced the life history by rearing the insect from the egg in the laboratory and by locating eggs, larvae, pupae, and adults in their natural habitat. Thus he demonstrated a typical complete metamorphosis cycle for this insect. At a daytime average temperature of 72 F and a night-time average of 65 F, he observed an egg incubation period of 2-3 days, a larval period of 14-21 days, and a pupal period of 9-13 days. Newstead fed his larvae on moist sheep manure. He found if food was allowed to partly dry and the larvae were exposed to light the larval period was extended. He also observed the adults preference for resting in the sun in the daytime and their inclination to retire to sheltered beams in sheds at night. In addition, he described the gross appearance of larvae and pupae with great clarity. He was the first to record Stomoxys larvae in grass clippings and was greatly impressed by the apparent attraction response of gravid Stomoxys females to disturbed portions of decaying grass heaps.

Mitzmain (1913), working in the Philippines, contributed extensively to the bionomics of the stable fly, although in his report the temperature and development relationships are not always clear or are variable. However, under his conditions, females began depositing eggs at 9 days of age and single females laid up to 20 batches of eggs totaling 632 to 820 individual eggs. At a temperature of approximately 30 C eggs hatched in 10-26 hours. Mitzmain reported larval periods of 6-26

days but states that 7-8 days is usual under optimum conditions. The pupal stage was 5 or 6 days in all his tests and, thus, he reported life cycle spans of 12 to 35 days from egg to adult. He also noted that adult flies of either sex will feed 6 to 8 hours after emergence and that a longevity record of 94 days was established by a captive male Stomoxys.

Bishop (1913, 1913a, 1920(1926)) described the life stages from Texas specimens observed in August. When eggs were placed on any moist substance they hatched from 1 to 3 days later. The larvae developed at various rates depending on the food and moisture available but usually required 11 to 30 days. When fully developed, the larvae shortened and the outer cuticle hardened to become reddish brown puparia. The pupal stage required from 6 to 20 days. Bishop also stated that complete development from egg to adult could occur in 19 days but usually averaged 21 to 25 under favorable conditions. The longest period observed was 43 days, but he postulated that the cycle might take as much as 3 months in the winter. Caged adults survived a maximum of 23 days and laid up to 278 eggs. None of his papers, however, provide temperature data that can be correlated with the cycle time intervals.

According to Hearle (1938) adult flies first appear in Canada in the coastal sections of British Columbia in April and in the Prairie Provinces in May and produce a number of broods before cold weather in the fall. Usually the cycle from egg to egg is completed in 2 to 3 weeks. Adult flies have been known to live for more than two months and to lay several batches of eggs in this time.

In Florida, Simmons (1944) demonstrated longer larval and pupal

periods for flies reared in December and January than for flies held at the same temperature in May and June and showed a variable egg incubation period of 19 to 120 hours at a temperature of 28 C. Both in the laboratory and in the field he found larvae overwintered in the 3rd instar during periods when the mean maximum temperature was under 60 F, but ordinarily a few adult stable flies could be found throughout the winter. Whenever there was a period of 3 or 4 warm days a large emergence would occur. The maximum life span observed in captured adults during the winter months was 49 days. Under optimum spring conditions the minimum egg to adult cycle was 13 days.

James (1947) apparently used Bishops' life cycle data but added the comment that in cooler climates hibernation takes place in the larval or pupal stage while in warmer climates there is no true hibernation. Knipling and McDuffie (1956) state that the life cycle may be completed in about 3 weeks in summer.

Working in Uganda, Parr (1959) devised a constant-temperature and humidity room rearing technique in which the egg to adult cycle was completed in 11 or 12 days. He reported the room was set to maintain a temperature of 90 F and a relative humidity of 90%. However, in his later publication (Parr, 1962) on life history and behavior of Stomoxys, he reported a temperature of 80 F and 80% relative humidity in the same facility with essentially the same life cycle data; i.e., 1 day as egg, 8 days as larvae, and 2 to 3 days as pupae. In Parrs' excellent study of the life history of stable flies in his laboratory, he observed all viable eggs to hatch within 24 hours by the almost instantaneous exit of the larvae as they forced open the anterior flat plate of the egg. His larvae increased at a steady rate without any

apparent rest period at ecdysis, spending the first 24 hours in instar I, the second 24 hours in instar II, and the next 6 days in instar III. He designated the period of reduced growth (7th and 8th days) as the prepupal period. Complete formation of the pupae was reported to require about 18 hours and subsequent eclosion of the imago 48 hours after first formation of the puparium. The eclosion of the imago was observed to be a quick rupture of the puparium and a rapid (average 22.4 seconds) exit of the fly. The fly moved about rapidly for up to 15 minutes and then remained stationary for 7-8 minutes. During this latter period the wings were extended, the ptilinum reduced and the general integument hardened. Further observations indicated mating took place when the flies were almost exactly 6 days old and the first eggs were laid at about 7 1/2 days of age.

Hoffman (1965) reviewed the literature covering laboratory rearing of stable flies and also described the 17 day egg to adult cycle of his own controlled environment colony. Apparently most of the controlled rearing has been conducted at lower temperatures than those reported by Parr, as egg to adult cycles are usually given as 15-25 days.

In 1966 Jones reviewed stable fly colonization and rearing techniques and described his experiences with a laboratory colony at Lincoln, Nebraska. He correlated room temperatures with development time in days as presented in the following tabulation:

Stage of Development	15.5 C	21.1 C	26.6 C
Incubation of egg	2	1	1
Larval	18	13	7
Pupal	8	7	7
Preoviposition of adult	18	9	6

Biology and Behavior

Eggs - The eggs of Stomoxys are apparently not deposited in any specific pattern or quantity. Simmons (1941) found them scattered individually and in irregular clusters throughout favorable media but not cemented together or to the medium. In cages, when no medium was available, the flies deposited at random throughout the cage. Up to 94 eggs were observed by Mitzmain (1913) to be deposited at one time by a single female. The same author reported that a total of 632 eggs were collected from one female and that she contained additional fully developed eggs when she died. Killough and McKinstry (1965) verified these data with a female they were studying that laid 602 eggs during her lifetime and contained eggs at death. In general, however, total egg production for a female will probably average 300-400 as demonstrated by Parr (1962), and these will be laid in 10-12 batches of about 35 eggs each.

The egg is sensitive to desiccation and will not long survive dry conditions. Invaribly the egg is deposited in moist media and usually below the exposed surface. Mitzmain (1913) reported killing the embryos in eggs by exposing eggs for 1 hour to air on a dry surface at room temperature. Todd (1964) observed females to lay eggs on the top surface of ensilage only if the ensilage were moist; otherwise, the flies penetrated to whatever depth required to place the eggs in a moist environment.

According to Mitzmain (1913) the ova were very sensitive to changes of temperature, light, and humidity. Incubation was lengthened to fully double its normal time by lowering the temperature or by withdrawing the moisture from the surrounding medium. At a temperature of

30 C, eggs hatched in about 20 hours, but at 20 C, eggs hatched in from 48-60 hours, depending on the humidity. Melvin (1931, 1934) observed eggs hatching in 32-35 hours at a temperature of 25 C and in 25-28 hours at 30 C. Exposure to light also influenced the metamorphosis. Eggs kept in the dark hatched 4-6 hours sooner than those of the same batch, held at the same temperature, exposed to exterior light.

Larvae - The stable fly larva is apparently not a particularly discriminating feeder. It has been found naturally, or has been reared in a great variety of moist fermenting organic matter (Eddy, 1952). However, it does prefer loose or friable substrata and only occasionally are the larvae recovered from pure animal droppings (Bishop, 1920 (1926); Parr, 1959, 1959a; Todd, 1964).

Larvae are responsible to conditions of light, temperature, humidity, or vibration (touch). Newstead (1906) noted that larvae matured at a slower rate when exposed to light and that they exhibited a strong negative phototrophism when their medium was disrupted and under these conditions would rapidly burrow into the medium and out of the light. The larvae can tolerate excessive moisture almost to the point of submersion but become inactive and often pupate early if their environment becomes dry (Bishop, 1913a). At temperatures under 60 F, the larval activity slows down and the organism may live for several weeks in this condition; even short periods of 30 F, temperatures did not kill the larvae in nature (Simmons, 1944). On the other hand, at air temperatures of 90 F or above the larvae often migrate to cooler places and even have been observed leaving the interior of media and going out into the light (Hoffman, 1965).

Mitzmain (1913) has reported observing cannabalism among stable

fly larvae; but the conditions under which the act occurred placed the larvae under serious stress from lack of moisture. According to Newstead (1906), larvae are repelled by a sudden jarring of the medium or any direct probing of the integument.

Pupae - The pupa is an immobile transition stage that is less affected by external environment than any other form of the insect, but like the other stages its development is retarded by lower temperature; and a temperature of 43 C will kill the developing imago (Mitzmain, 1913). The same author reported pupae would not emerge if held in water and that exposure to light extended the pupal period.

Imago or Adult - A detailed description of adult emergence from the pupal case, the early frenzied running about of the new adult, the wing expansion, the proboscis and exoskeleton hardening, and the preparations for the first flight are graphically presented by Newstead (1906). Mitzmain (1913) found that the development and activity of the fly through the stages described by Newstead required about 30 minutes and thus the flies were incapable of feeding, at least, for that period. During the next 1-6 hours the flies were observed to make short flights that often terminated at the point of origin and also spent long periods of time "grooming" themselves with their hind or fore legs.

Although Newstead (1906) did not observe Stomoxys actually in the act of feeding on animals, he made the point that blood was their normal diet; he then related observations of flies removing moisture from manure, a sugar and water solution, and from a fetid potato. A vivid description of the feeding act was given by Mitzmain (1913) from watching several stable flies feed on his person. The flies alighted on his

arm, scraped the skin with their labellae and started to probe within an interval of 10 seconds. Shortly, the proboscis was inserted and the body began an aspirating movement. As the abdomen filled, small droplets of fluid were exuded from the anus. Flies took blood from a minimum of 1 minute 30 seconds to a maximum of 12 minutes 40 seconds. Males usually required under 4 minutes. Krijgsman (1930) recognized the sequence of events in feeding as: (1) positive taxis, (2) extension of proboscis, (3) probing response, and (4) ingestion.

In feeding tests of Stomoxys on various animals, Mitzmains' flies feed on 17 species as diverse as horses, chickens, bats, and lizards. When only a few flies are attacking a bovine host, the flies tend to concentrate on the lower portion of the forelegs, but feeding may occur on any exposed part of the body (Bishop, 1913a; United States Department of Agriculture, 1953; Horsefall, 1962). Parr (1962) fed hungry flies on ox-blood and found that the average fully engorged fly consumed 25.8 mg of blood or about three times that of its own body weight. Several authors credit the fly with taking one blood meal each day but Bishop (1920(1926)) suggests they often feed more than once and that they apparently require three or four meals before they deposit eggs. Parr (1962) suggested the flies seeking a host were attracted to black color and moving objects, and that color and odor were important only at close range. Bishop (1913a) also indicated that finding the host seemed to be a phenomenon of sight. Once located on the host, probing is induced by a group of stimuli which are token indicators of the presence of blood; e.g., ammonia, and these lead to the further stimuli that promotes biting (Hopkins, 1964).

According to Todd (1964) Stomoxys attacking cattle characteristi-

cally alights with the head uppermost; is disturbed easily before inserting the proboscis; but once feeding has begun, is very difficult to dislodge. After having fed to repletion, the flies seek a nearby object or plant that will provide climatic comfort and protection and there they remain more or less sedentary until the blood meal has been digested.

Whole blood has been indicated to be an essential element of the stable fly diet by Glaser (1923). The same author demonstrated that neither serum nor red cells fed separately would induce egg deposition. Later Tuttle (1961) fed stable flies extracted serum and red cell components blended in various combinations and reported that both elements were essential in egg deposition, except that dextrose could be substituted for the red cell fraction of beef blood to induce oviposition. Tuttle also reported that blood diluted by 50 percent cannot support life normally or result in normal egg production. Flies were fed room temperature or refrigerated blood by Simmons (1944) without ill effects and Bishop (1913) reported on one fly that imbibed 14 full blood meals. Hoffman (1965) has reported daily feedings for 30-60 days.

The stable fly is a strong flyer and has been observed to travel long distances. Bishop (1913a) has noted it in pursuit of moving horses, automobiles, and passenger trains. The United States Department of Agriculture (1941) has reported a marked specimen was recovered 52 miles from the release point and that the flies have been commonly seen on ships several miles offshore. Eddy et al. (1962) recovered marked stable flies 5 miles from the point of release in 2 compass directions within 1 hour and 45 minutes of the time of release. Apparently, there are no data concerning the specific time of life a

stable fly may have migratory tendencies or if movement relates only to the environment in which the fly finds itself without regard to age.

Mating, as previously indicated, usually takes place about 6 days after eclosion from the pupae although Harris (1966) has observed one mating of 2-day old flies. Killough and McKinstry (1965) reported that 1-day old males can mate. The male was observed by Mitzmain (1913) and Parr (1962) to be the aggressor and the same male may, in captivity, make repeated attacks upon a virgin female until he is accepted. After copulation the male may attempt further attacks on the same female, if other females are not present; however, if he is repeatedly rejected he eventually turns his attention elsewhere.

In nature, copulation usually takes place off the host and upon completion of the act the male flies off while the female often remains at the spot for as much as 30 minutes (Parr, 1962). Males were reported by Harris (1966) to inseminate as many as 9 females and to average 6.13. His data also strongly indicates that female stable flies will probably not remate if sperm is transferred on the first mating.

Approximately 48 hours after copulation at ambient temperatures of 70-80 F, the female will seek out a location to deposit her first clutch of eggs (Parr, 1962). Newstead (1906), Bishop (1913a) and Todd (1963) observed gravid females attracted to decaying grass or silage and concluded they were attracted by the odor. In Florida, Simmons (1944) noted that flies would lay eggs only on seaweed that was freshly deposited on the beach or up to 1-week thereafter, suggesting that both odor and heat of decomposition were necessary because the mass still had odor after a week, but was no longer warmed by bacterial decay.

Control

The present paper is not intended to be a treatise on control of the stable fly but a few remarks concerning the status of control efforts are appropriate to complete the background information. As recent as 1963, DeFoliart observed "the stable fly...has remained largely untouched by control methods". Bishop (1913, 1920(1926)) recommended meticulous sanitation and elimination of breeding (larval) sites as the first principle of stable fly control. He also recommended fly traps in barn windows and placing manure within large box-like, fly traps. Finally, he found some odoriferous products such as a mixture of fish oil, pine tar, oil of pennyroyal, and kerosene would provide short time repellency if applied to those portions of an animal not covered by a blanket or net.

Nearly every publication on stable fly control since those of Bishop has continued to stress sanitation as part of the suppression program. In 1941 the United States Department of Agriculture recommended cattle and horses be sprayed at frequent intervals with pyrethrum products containing 5 to 10 parts of concentrate to 1 part of light, refined oil; also a combination of creosote oil and fuel oil applied to accumulations of organic matter or seaweed.

Hearle (1938) stressed removal or destruction of rotting hay or straw piles and suggested that animals be fitted out with canvas trousers from the knees down and/or provided darkened shelters where flies would cease to annoy. The repellency of pyrethrum-thiocyanate oil sprays was evaluated by Howell and Fenton (1944) by spraying cattle twice daily with about 15 ml of various concentrations of the sprays and, although reduction of horn flies was marked, stable flies continued

to attack the cattle except for a sharp, but temporary, decline following the afternoon spraying.

Fly control by use of synthetic organic insecticides was initiated in the late 1940's and in 1952 Eddy recommended a combination of methods to reduce the stable fly that included: (1) Destruction of breeding places, (2) application of a residual organic insecticide to buildings, sheds, corrals and other fly resting places, and (3) application of insecticides - especially pyrethrins - to the animals. However, Dicke (1953) wrote that stable flies were hard to kill with residual sprays in Wisconsin and that sanitation was the most practical means of controlling Stomoxys in that state. Also in 1953, the United States Department of Agriculture published a bulletin detailing insecticide and sanitation recommendations similar to those of Eddy.

Several organic thiophosphate insecticides, including chlorthion, diazinon, isochlorthion, and pirazinon, were applied as residual insecticides on Iowa farmsteads by Dahm and Raun (1955) and, although they obtained good reductions of house flies, stable fly reductions were erratic. Abundant fly breeding in trench silos apparently accounted for much of the re-infestation.

Emphasis was again placed on sanitation by Knipling and McDuffie (1956) in an article in the Yearbook of Agriculture. They stated that the greatest returns for the effort often came from preventing the accumulation of wastes and manure and that then the insecticides properly used could usually further reduce the problem.

The daily application of pyrethrum insecticides to cattle by use of a treadle-type automatic sprayer was reported by Cutkomp and Harvey (1958) to give 70-75% reduction of stable flies and was given credit

for the increased weight gains of the animals treated. Cheng (1958) reported similar positive data from the use of an electric-eye controlled automatic sprayer to dispense deet or pyrethrum formulations onto beef cattle in Pennsylvania.

One completely successful insecticide treatment was reported by Parr (1959) from Africa after he treated foliage surrounding an isolated cattle boma with a 4% chlordane soil spray. This situation was apparently the only source of new flies in the area. Todd (1960, 1964) in New Zealand reported several failures by insecticides, principally because of tremendous reinfestation pressure from silage trenches in the experimental areas.

METHODS AND MATERIALS

Test Animals, Insects, Rearing, and Facilities

All of the laboratory portions of this study were conducted in the facilities of the United States Department of Agriculture, Biting Fly Laboratory, Kerrville, Texas. This facility is equipped with temperature and humidity cabinets, animal and insect holding rooms, routine insect handling equipment, and highly specialized stable fly rearing and experimental rooms, as described by Hoffman (1965).

The Kerrville strain of the stable fly, Stomoxys calcitrans (Linnaeus), was used as the test insect for the current study. This strain has been reared continuously for at least 10 years at Kerrville without addition of new stock, and the rearing technique, as described by Hoffman (1965), was used throughout the current research.

In feeding tests requiring host animals, 1500-1800 pound Hereford steers were utilized. These cattle were part of the station herd and were animals often used in other biting fly research studies. During tests, the steers were confined to 9 X 10 X 8-foot, part-screen, large animal rooms under regulated temperature and lighting conditions. When not "in test" the animals were either confined to outdoor feed lots or were free to roam a 500 acre pasture.

Testing Procedures

Egg Studies - The number of eggs deposited, the percent hatch, and the length of the egg stage were determined for the colony flies

by placing 200-300 newly emerged adults in a holding cage (Figure 1,A) for a period of 6 days, then selecting 20 females from the cage at random to be placed in individual egging cages (Figure 2,E). Eggs were collected twice daily under the cages on damp, black cotton cloths and any adhering to the cage were removed with a camels hair brush. Tests were continued until all flies died a natural death. Eggs of each female were transferred to separate damp, black cloths and placed in small petri dishes to be incubated at a temperature of 78 F ± 2°. The eggs were examined for hatch at 24, 26, 28, 30, 32 and 48 hours later. Three replicates were completed.

The resistance of eggs to drying was considered by isolating eggs that were under 4 hours of age on dry glass slides, then placing the slides in a constant temperature and humidity cabinets at either 78 F ± 2° and 50% or 78 F ± 2° and 80% temperature and relative humidity, respectively. At periods of 15, 30, 45, and 60 minutes, 20-egg lots were removed and placed on damp, black cloth in petri dishes as indicated above, to be examined 24 and 48 hours later for hatching. Three replicates were completed.

Tolerance to submersion was considered by placing an estimated 1000 eggs in water in a 50 ml beaker and at 30 minute intervals, up to and including 6 hours removing 20-egg lots to petri dishes as described above. The eggs were examined at 24, 48 and 72 hours for hatching. Three replicates were completed.

Larval Studies - Length of larval life of the colony flies was determined by placing 50 newly emerged 1st instar larvae onto regular CSMA[1] fly larvae diet contained in 800 or 1000 ml beakers and placing

[1]Laboratory larval diet prepared by Purina Milling Corp.

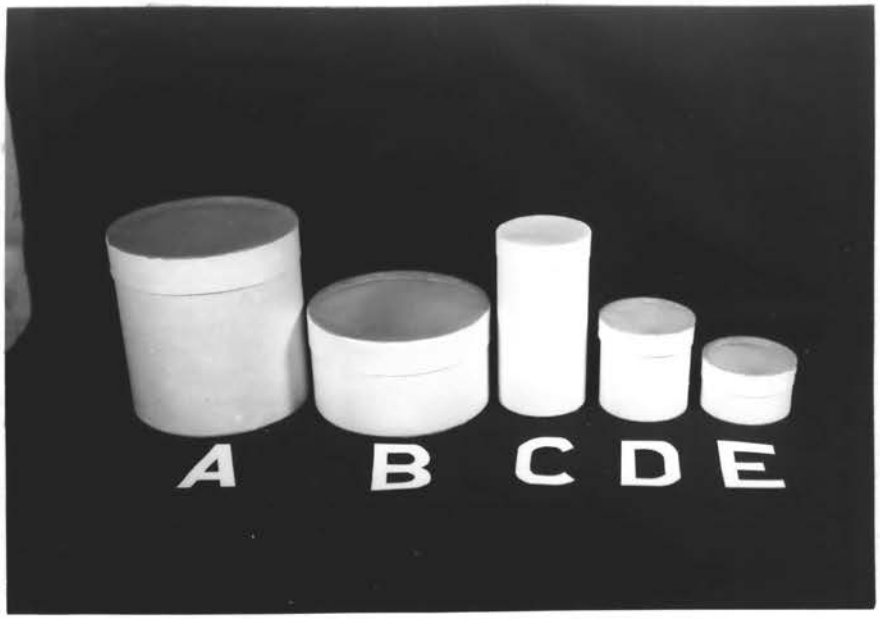

Figure 1. Stable Fly Holding Cages for Laboratory Studies.

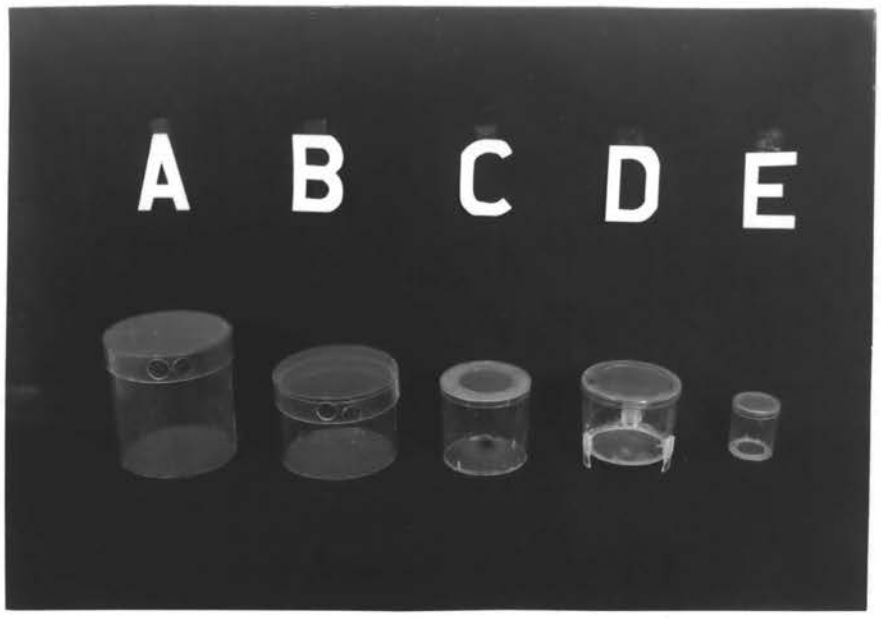

Figure 2. Plastic Laboratory Test Cages.

the beakers either at room temperature (78 F ± 2°) in the stable fly rearing room on in constant temperature cabinets at 70 F or 90 F. The effect of crowding was considered by placing 50-500 newly emerged larvae onto a medium prepared by blending 30 grams of CSMA medium and 70 ml water. Each test unit was maintained in a 1000 ml beaker and kept at room temperature in the stable fly colony room. Progress of larval development was observed daily and the number and size of those larvae pupating were noted.

Moisture level requirements of larvae were studied by placing 25 newly hatched 1st instar larvae on 30 grams of CSMA medium blended with 0-220 grams of water in 100 ml beakers. Larvae were allowed to pupate and the adults to emerge to obtain an estimate of the total effect. Five replicates were completed.

Larval tolerance to submersion in water (Figure 3,B) was estimated by placing 3rd instar larvae into water at room temperature and then, at various intervals between 15 minutes and 21 hours post-submersion, 25-50 larvae were removed, placed into CSMA medium in beakers and observed for survival, pupation, and adult emergence.

Pupal Studies - To determine the length of the pupal period at 70, 78, and 90 F, several hundred pupae, that were known to have pupated in a 2-hour period, were washed from the same rearing pan, divided into 3 equal lots, and each lot placed in a 1/2-pint paper carton. The cartons were each placed in an emergence cage (Figure 1,A) and one held at each of the 3 indicated temperatures for a period of 7 days. All adult flies in the emergence cages were removed twice daily (8 a.m. and 4 p.m.) and the number and sex recorded.

The effect of water immersion on pupae was determined by placing

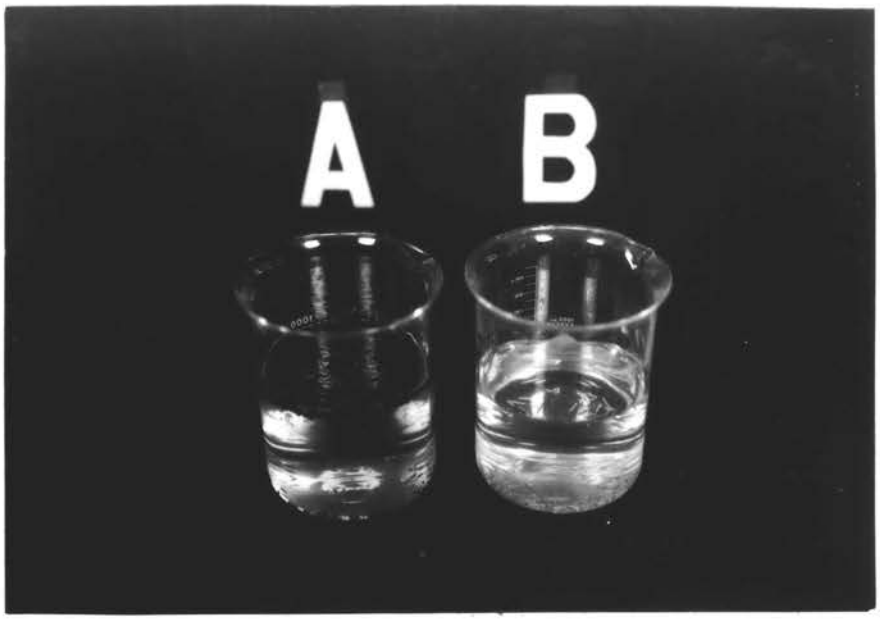

Figure 3. Larval and Pupal Submersion Beakers.

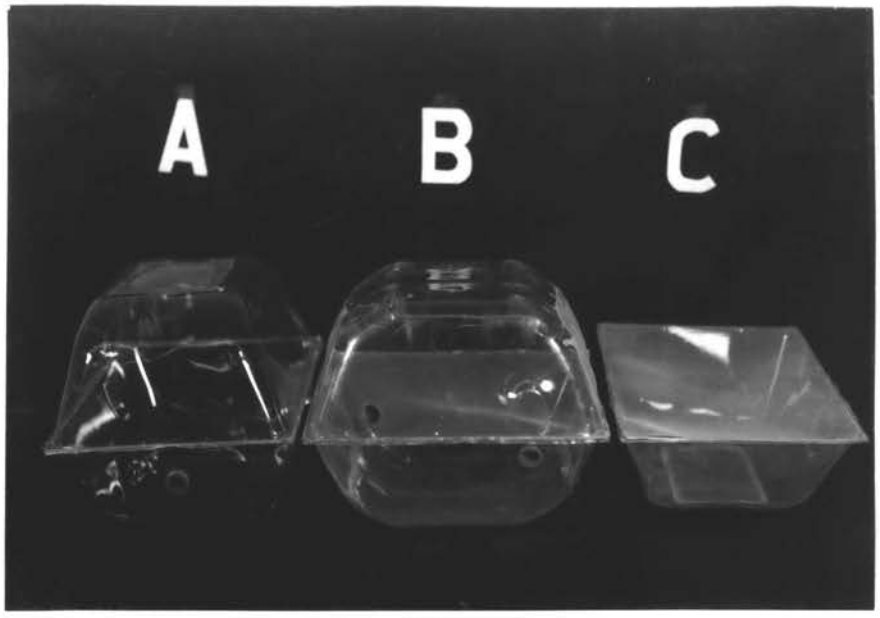

Figure 4. Stable Fly Activity Cages.

pupae known to be at least 12 hours old into beakers of water at room temperature and subsequently removing lots of 50 at various time intervals between 16 and 360 hours thereafter. The removed pupae were placed on damp sand in beakers and records of eclosion were kept.

The eclosion of the adult from the puparia was studied relative to the pattern of emergence within a time period of 5 days. Eggs laid within a 30 minute period were gathered from a colony egg-laying cage, placed in a pan of CSMA medium and reared in the laboratory colony room until 24 hours after the 1st of their number began to pupate. The pupae were removed by flotation from the pan and separated into 3 lots of about 1500 pupae each. Each lot was placed in a 1/2-pint carton (Figure 1,E) and then the small containers were placed in individual 1-gallon paper and screen emergence cartons (Figure 1,A). One carton was placed in a room that had 24-hour fluorescent lighting; one was placed in a light-tight cabinet in a dark room; and one was placed out-of-doors exposed to typical September weather conditions (See Figure 8). The two indoor lots of pupae were exposed to relatively constant 78 F temperatures.

As the flies began to emerge from the puparia, they were removed from the emergence cartons on the hour, every hour around the clock, counted, and sexed. To remove the flies without altering the light conditions, carbon dioxide gas was turned into the emergence cartons while the cartons were kept in their respective locations. The anesthetized flies were dumped into another cage and removed to a separate laboratory room for examination.

At some point in the development of stable fly pupae, the organism becomes capable of floating on water rather than being submerged like

the larvae (Figure 3,A and B). This point in time was approximately established by placing pupae of various developmental ages into beakers of water at room temperature. The zero hour of development was arbitrarily placed at that moment the prepupae completely assumed the typical barrel-shape and became immobile. It is recognized that this judgement is crude and could easily be plus or minus 15 minutes. Nevertheless, using this criteria, numbers of pupae were placed into the beakers of water at 30 minute intervals, up to and including a 4 hour interval, and percent flotation data for each interval established.

Adults - Observations of the general activities and attitudes of adult stable flies were recorded for flies housed in the various plastic and screen constructed cages shown in Figure 4. Similar data were obtained for flies released into 9 X 10 X 8-foot, part-screen, fluorescent lighted, large animal rooms.

Diet and feeding studies included experiments on the quantity of blood a male and female will take from a bovine host and as citrated blood from small synthetic sponges and cotton pads. In all trials, sexed, unfed flies were weighed on a torsion balance in lots of 25, allowed to fully feed, and then were weighed again to determine the quantity of blood ingested. Data on the time of day flies fed when in captivity and how often they would accept food was also obtained by observing flies housed individually or in small groups in plastic cages like those shown in Figure 2, C and E. Small, mixed-sex groups of flies were offered diets of saturated sugar water, plasma, 50% plasma plus 50% normal saline, serum, 50% serum plus 50% normal saline, bovine red cells suspended in normal saline, normal saline, and whole bovine blood to determine the stable flies ability to survive on other than

whole blood. The flies were fed fresh quantities of the various diets twice daily (8 a.m. and 4 p.m.) on small cotton pads and dead flies were removed from the cages once each day. Cages and egging pads were examined closely for eggs and those eggs found were transferred to damp, black cloths and kept in petri dishes, where they were watched for development.

The sexual or mating activity of both sexes of the colony flies was studied to determine the number of times each would mate, the time between matings, the time in copula, the age requirements, the preferred time of day, and the activity of each participant during and subsequent to mating. Individual 1-day old males were placed with 20 newly emerged virgin female flies for a period of 6 days in 1-quart paper and screen cages (Figure 1,C) for the male "number of matings" trials. After 6 days, the females were removed from the mating cages and each placed in an individual egging cage that was kept in contact with a damp, black egging cloth. Eggs produced were placed in petri dishes as previously described and hatch was recorded. Immediately after the first 20 females were removed from a mating cage, 20 more 4-day old virgin females were put into the cage with the male. Forty-eight hours later these females were removed and replaced with 20 more. This process was continued until the male died. Number of matings by females was determined by continuously observing the activities of flies in plastic cages (Figure 2,A). Each of the cages contained 1 virgin female and 10 males at the beginning of the observation period. All other mating activity observations were made by watching the activity of flies in plastic cages similar to Figure 2,C, except that minimum mating age studies were conducted by placing separate cages of

5-days old virgin females with males known to be 0-8, 8-16, 16-24, 24-32, 32-40, 40-48, 48-56, 56-64, or 64-72 hours old. Females from each combination were separated out into individual egging cages and any eggs recovered handled as previously described. The procedure was reversed to obtain information for the females; that is, 5-days old males were placed with females that were known to be of the ages indicated above. The females were removed from the mating cages at the end of their 8 hours and egged separately as before.

Experiments to compare the numbers of eggs mated and unmated females would lay was accomplished by separating about 100 newly emerged flies by sex into 2 cages of females and 1 of males. Into one cage of females, 25 males were introduced while none were put in the second cage. At 6 days of age 10 females were selected at random from each cage and each fly placed in an individual egging cage over an egging pad. Eggs were removed and counted twice daily until all flies died. Three replicates were completed.

Life expectancy of adult flies in captivity was investigated by separating the sexes at emergence and then placing flies in cages (Figure 1,C) at ratios beginning with 1 male to 5 females and continuing consecutively through 15 males to 5 females. Death of flies was recorded once each 24 hours and the dead flies identified as to sex. Two series of tests were conducted.

Although stable fly females do not appear to be especially gregarious in nature, a study was conducted under laboratory conditions to determine if individually housed or combinations of flies would lay the greater number of eggs. For these tests, 20 1/2-pint cages were placed on a shelf in the fly rearing room to house the flies. Mated stable

flies were placed into the cages, 1 in cage No. 1 up to 20 in cage No. 20. Egging pads were kept under each cage and the eggs deposited were removed and counted daily. Death of flies was noted and production records were kept on a per fly basis until all flies died.

The attractions of color in selection of a resting site in large animal screened cages (9 X 10 X 8 feet) was investigated by hanging 1" X 2" X 3' painted sticks from the cage ceiling; each stick was located at a distance of 18 inches from an enclosed glass fluorescent light and spaced equidistant from one another. The sticks were painted black, white, brown, blue, green, or red with non-glossy enamel paints. At 10 a.m. about 1000 stable flies were released into the cage at the floor level and every 15 minutes for a period of 2 hours a rapid count was recorded of the number of flies resting on each colored stick. The counts for any one color were totaled to provide one figure for each color. The test was replicated 6 times so that each stick was suspended in each location once during the course of the experiment. This makes a Latin Square design in which the columns are positioned in the room and the rows are replications.

Descriptions and Conditions of Field Study Area

Field investigations were conducted entirely in Kerr County, Texas, a highly irregular, mostly rocky semi-arid region that is part of the Edwards Plateau or "hill country" in south-central Texas (Figure 5). The rough, rocky areas support a grass complex of bluestems, indiangrass, wild rye and buffalo grass and have a brush overstory of live oak, shinnery oak, juniper and mesquite. One major permanent stream, the Guadalupe River, provides water for a small hay and grain acreage in the narrow valley through which it flows. Other streams of the

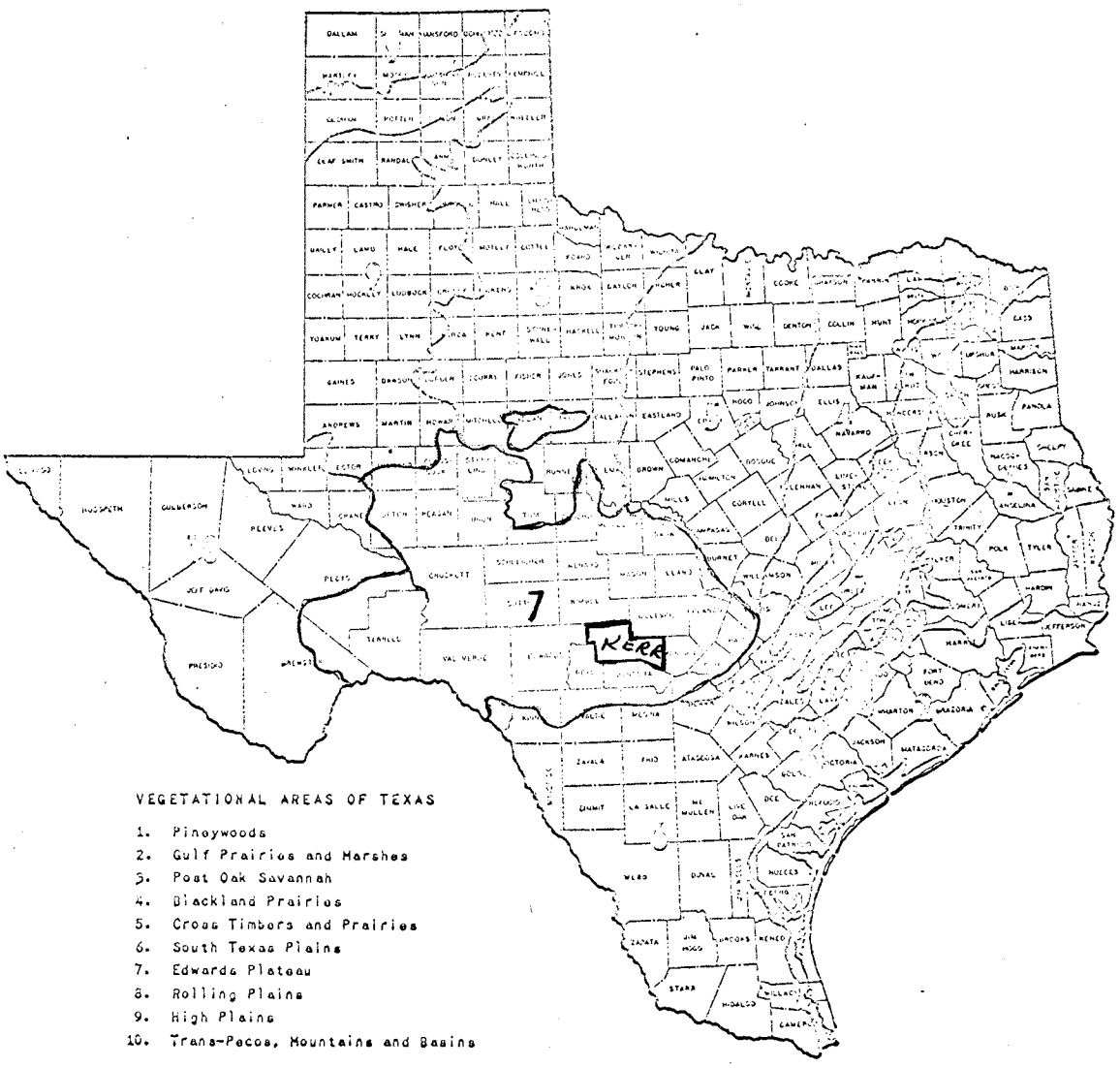

Figure 5. Map of Texas Indicating the Vegetational Ecological Areas and Kerr County.

country are spring fed with very limited flows or are intermittent, depending on rainfall. In general, livestock is watered out of dirt or metal tanks located near drilled wells. Summers are normally hot and dry while the seasonal rainfall pattern shows typical highs in May and September. Some years the principal high covers the latter part of August, September, and October, providing a combination of warm weather and substantial rainfall, as was the case two of the three years of the present investigation.

Agriculture in Kerr County is primarily a livestock on native grass situation with beef cattle, Angora goats, and sheep the major animals involved. Stocking rates vary from 1 to 10 animal units per 100 acres. Except for two small beef feed lots and several small dairies there are no abnormal concentrations of livestock in the county. Several commercial summer camps and dude ranches operate from mid-June to mid-August along the upper Guadalupe River valley and gorge in the southwestern part of the county and each of these have a number of horses and mules that are kept in corrals or pastures. Rarely are animals of any kind kept routinely in a barn or stable.

A small herd of bison that receive supplemental feed, and the stable fly rearing laboratory of the United States Department of Agriculture provide two atypical potential sources of stable flies in the county.

Although cursory surveys of the entire county were performed at irregular intervals to determine presence and abundance of flies, the principal observations were made at 21 selected properties at which adult stable flies or potential larval sites were seen during the surveys. The surveys were conducted by random visits to all areas and

ecological situations represented in the county. Livestock were observed - often with the aid of binoculars - for fly activity; barns, sheds, fences and foliage were inspected for resting flies; and potential larval habitats were examined for larvae.

The 21 principal locations included 10 small dairy farms, 2 small beef cattle feed lots, 2 cattle ranches, 2 horse ranches, 1 poultry farm, 1 dude ranch, and 3 general livestock ranches. All of these locations were similar in that each had 1 or more small, shed-type buildings or shelters and an open water source closely grouped in a space of 1 acre or less (Figure 6). In addition, each of the dairies had a small pit-type, concrete block milk parlor and the poultry ranch had 2- 20 X 60 ft birds on the floor, litter-type houses. Each of these small, artificial "oases" was surrounded by typical dry-land pasture, except that one dairy had about 100 acres of irrigated river bottom pasture nearby. In general, the terrain, meteorlogical conditions, and livestock practices of Kerr County are not typical of those described by authors as suited for stable flies.

Field Study Observations

Stable fly biology and behavior were determined among wild flies by close visual observation and subsequent recording of the activities of the flies in nature in the various locations and under the general conditions indicated above. Specific conditions of time of day, temperature, moisture, light and immediate environmental circumstances were noted. Egg and larval studies were accomplished by collecting and counting eggs immediately after females laid same, then a known number were placed in a vessel containing a quantity of the same larval medium the females had originally chosen and the vessel was placed in

Figure 6. Typical Kerr County Dairy Dry-Lot.

the immediate area of the natural media. Egg hatch and larval development were recorded.

Where adequate numbers of stable flies occurred, the detailed conditions of the immediate habitat varied primarily with the use to which the properties were put. For example, all the horse ranches had an open, dry corral as their central feature with little or no shade from trees and usually no free access to nearby open sheds. In the corral there was usually one small metal water tank that leaked or overflowed enough to wet the ground area adjacent to the base of the tank. Horses were confined to the corrals only when being used daily; at all other times, they could enter or leave by an open gate that led to a "trap" pasture. Thus, manure rarely accumulated in the corral areas and the "trap" pastures were always of a size that allowed the animals to move freely. Dairies, on the other hand, invaribly had feed bunks surrounded by a wet or damp mass of hay, manure and dirt, calf pens, 1 or more large leaky water tanks, a loafing shed, a milk barn from which manure was flushed with quantities of water into an open ditch, and a concentration of cows in a drylot or pasture that seldom exceeded 5 acres in size.

RESULTS AND DISCUSSION

Laboratory Studies

Eggs - The number of eggs laid by colony-reared female stable flies is given in Table I for 20 individuals. Most of the females laid their first eggs on the 7th or 8th day after eclosion from the pupae and usually they laid some eggs on 5 or 6 out of the first 7 days after laying began. After day 7, egg deposition became erratic and some flies skipped up to 6 days before they laid again. One female of the 20 laid periodically for 31 days, while at the other extreme, one laid a single batch of eggs when she was 25 days of age. There also appeared to be a tendency to alternate between laying large and small batches of eggs. In this particular test series, the total eggs per fly varied from 22 to 307 with an average of 183. The average number of eggs hatching was 79.95%. The egg production figures fall way short of the 600+ maximum reported by Killough and McKinstry (1965), but, I believe, the numbers are representative of normal fly production.

TABLE I

NUMBER OF EGGS LAID AND HATCHED PER FEMALE STABLE FLY[1]

Fly Number	Total No. Eggs	Egg Hatch No.	Egg Hatch Percent	Fly Number	Total No. Eggs	Egg Hatch No.	Egg Hatch Percent
1	207	182	87.9	4	213	190	89.2
2	241	222	92.1	5	307	261	85.1
3	22	0	0.0	6	98	72	73.5

TABLE I (continued)

Fly Number	Total No. Eggs	Egg Hatch No.	Egg Hatch Percent	Fly Number	Total No. Eggs	Egg Hatch No.	Egg Hatch Percent
7	119	99	83.2	14	161	132	82.0
8	269	200	74.3	15	253	221	87.4
9	235	214	91.1	16	187	106	56.7
10	210	155	73.8	17	171	155	90.7
11	190	171	90.0	18	139	130	93.5
12	215	187	87.0	19	108	98	90.7
13	151	147	97.4	20	168	159	94.6

[1]Tallied only for flies that lived at least 20 days.

Eclosion of the larvae from the egg at flyroom temperature (78 F ± 2°) began shortly before the first observations were made at 24 hours as indicated by a small number (4.1%) of empty egg cases. Table II gives the number and percent of total egg hatch observed in 3101 eggs up to the hour indicated and between any 2 observations.

TABLE II

EGG HATCH RELATIVE TO TIME AND NUMBERS

Hours After Eggs Laid	Hatched	Percent of Total	Hatched Between Observation	Percent of Total
			127	4.1
24	127	4.1		
			444	14.3
26	571	18.4		
			862	27.7
28	1433	46.2		
			841	27.1

TABLE II (continued)

Hours After Eggs Laid	Hatched	Percent of Total	Hatched Between Observation	Percent of Total
30	2274	73.3		
			418	13.5
32	2692	86.8		
			409	13.2
48	3101	100.0		

Fifty-four and eight tenths percent of the eggs hatched between 26 and 30 hours after being deposited and the mean occurred at about 28 hours and 17 minutes.

Egg hatch, as determined by the technique described for this paper, may be affected adversely by the handling required to transfer the eggs to egging dishes, by selection of eggs from a location that allowed the eggs to desiccate, or because observations were discontinued at 48 hours. No doubt, these factors made some deleterious contribution to the percent hatch obtained, but, I believe, such losses were held at a minimum and that Table II is a reasonable representation of the hatch to be anticipated from a batch of eggs laid in any normal location.

TABLE III

PERCENTAGE HATCH OF EGGS EXPOSED TO AIR DRYING AT 78 F ± 2°

Minutes Exposed to Drying	Relative Humidity 50%	80%
15	57.1	68.2
30	6.4	21.4
45	0.0	3.5
60	0.0	0.0
0 (control)	82.3	87.0

Eggs exposed to air lost moisture rapidly unless protected from drying. Data are presented in Table III for eggs exposed to 78 F ± 2° at 50% and 80% relative humidity and, although, those eggs held in the high humidity survived better than those held in the low humidity, only a few survived more than 30 minutes. In nearly all cases, however, when the eggs were returned to the moist environment of damp cloths in petri dishes they quickly regained moisture and became turgid. Thus, the eggs again had the gross appearance of a normal egg. Some eggs exposed to drying for 60 minutes collapsed completely and did not regain turgidity.

Eggs were tolerant to submersion in water, although submersion apparently delays hatching. Nevertheless, continuous submersion for 5 hours or longer apparently was fatal to the embryoes. Table IV presents the data in terms of the percentage hatch 24, 48, and 72 hours after removal from the water.

TABLE IV

EFFECT OF SUBMERSION OF EGGS ON HATCHABILITY

Minutes of Submersion	Percent Hatch At Indicated Hours After Submersion		
	24	48	72
30	1.5	67.0	75.5
60	0.0	65.5	71.0
90	0.0	51.5	72.5
120	0.0	42.0	70.0
150	0.0	49.0	62.0
180	0.0	43.5	57.5
210	0.0	36.0	47.5
240	0.0	14.5	28.0

TABLE IV (continued)

Minutes of Submersion	Percent Hatch At Indicated Hours After Submersion		
	24	48	72
270	0.0	15.5	27.5
300	0.0	0.0	0.0
330	0.0	0.0	0.0
360	0.0	0.0	0.0
000 (control)	12.5	78.5	79.5

Larval Studies - The time larvae require to complete development is affected by several environmental factors. Of these factors, temperature is probably one of the most important as it affects both the larvae and the condition of the media. The following tabulation gives the approximate range of time required for larvae to develop from newly hatched first instar to formation of the pupae:

Temperature of Cabinet ^{o}F	Range In Hours To Complete Larval Development
70	336--384
78	240--264
90	216--240

All of the time intervals reported here are far less than Melvin (1931) found in his studies. It seems probable that other factors, especially the medium, are responsible. Melvins' larval diet consisted of oat hulls, while the diet used in these tests was standard CSMA laboratory fly medium.

Crowding of larvae results in a smaller organism at time of pupation, a reduction in the number of those larvae that complete develop-

ment, a small pupa, and an inferior adult. Some of the overcrowded larvae attempted to escape the medium, some "milled" about on the surface of the medium, and others appeared to develop to about one-half normal size, become lethargic, and remain static in growth for an extended period of time. Lack of sufficient food is, no doubt, one of the causes for the reaction, but it seems reasonable that physiological effects brought about by insufficient oxygen or excessive environmental pollution by the larvae themselves may be important factors in the development of inferior larvae. Table V presents data of the effect on growth of rearing various numbers of larvae in a given amount of medium. The test was terminated 15 days after the larvae had been introduced even though beakers seeded with 250 or more larvae still contained some live, partially developed specimens. On the basis of this study it would appear that each gram of CSMA media should not be expected to provide nourishment or living space for more than 3 or 4 larvae under conditions similar to those described.

TABLE V

NUMBER AND WEIGHT OF PUPAE REARED FROM 30 GRAMS OF MEDIUM SEEDED WITH VARIOUS NUMBERS OF LARVAE

Number First Instar Larvae Seeded	Resulting Pupae	
	No. formed	Average weight in mgms.
50	47	15.3
100	81	14.7
150	102	13.6
200	82	11.8
250	41	8.8
300	30	8.6
400	12	7.9
500	0	0.0

Larvae can apparently survive a wide range of moisture conditions and still produce normal sized pupae. Table XI gives data that indicate those larvae that lived in slightly damp to completely saturated CSMA medium produced, at least, a few mature pupae, even though the number of pupae produced at the two moisture extremes was greatly reduced. No larvae survived in media to which water was not added and only 5 of 125 survived the highest water to medium ratio of 220:30 grams. At the higher moisture rates of 200 and 220 grams of water the medium turned sour and mold formed. There was no indication that larvae which did survive and pupate were adversely affected as they produced normal numbers of adult flies, except that flies produced from the 30:10 CSMA-water ratio were small and did not survive long. One other effect of note was that as the moisture increased above 160 grams of water, the larvae matured more slowly.

TABLE VI

MOISTURE REQUIREMENTS OF STABLE FLY LARVAE[1]

Quantity in Grams		Resulting Pupae		
CSMA	Water	Number	Percent Pupated	Average weight in mgms.
30	0	0	0.0	0.0
30	10	33	26.4	8.5
30	20	73	58.4	14.9
30	30	66	52.8	15.4
30	50	88	70.4	15.5
30	70	73	58.4	15.6
30	100	69	55.2	15.6
30	120	81	65.0	15.4

TABLE VI (continued)

Quantity in Grams		Resulting Pupae		
CSMA	Water	Number	Percent Pupated	Average weight in mgms.
30	140	72	57.6	15.1
30	160	77	61.7	15.1
30	180	81	65.0	14.9
30	200	30	24.0	14.6
30	220	5	3.2	14.5

[1]25 larvae per test, 5 tests completed.

Third instar larvae are able to tolerate complete submersion in water for several hours without killing the organism. However, pupae and adults that are produced from the larvae decrease in numbers as submersion time increases. At approximately 17½ hours the mortality begins to increase rapidly. Submerged larvae actively move about for the first 15-30 minutes but by 45 minutes most of the larvae have become quiescent on the bottom of the beaker. Data for these tests are presented in Table VII.

TABLE VII

TOLERANCE OF STABLE FLY LARVAE TO SUBMERSION

Submersion Time		Percent Of	Percent Of	Percent of Pupae
Hours	Minutes	Larvae Revived	Larvae Pupating	Producing Adults
0	45	100	94	86
1	15	100	91	84
1	45	100	91	56
2	00	100	50	50
17	00	100	79	58

TABLE VII (continued)

Submersion Time Hours	Minutes	Percent Of Larvae Revived	Percent Of Larvae Pupating	Percent of Pupae Producing Adults
17	15	99	56	62
17	30	45	38	45
17	45	50	24	33
18	00	16	4	0
21	00	0	0	0

Pupal Studies - Like the other immature stages of the stable fly, the pupa responds to increased or decreased temperature of its environment by a lengthening or shortening of the pupal period. However, at the three temperatures used in the present tests, eclosion invariably "spread out" over a 4 day interval, although the bulk of the flies emerged during the 2nd and 3rd days of the interval. At all three of these temperatures, 89.4 to 94.6% of the pupae developed into flies. Sex ratio of emerging flies for the 78 F temperature was 15 males to 9 females during the 1st 4 hours of emergence. Thereafter, the ratio slowly changed to 10 to 9 females to males by the end of the second day, and 10 to 7.5 by the end of the 3rd day. In this series of tests, the overall sex ratio was approximately 54% females and 46% males. The following tabulation gives the approximate range of eclosion times for 70, 78, and 90 F in the tests discussed.

Temperature of Cabinet Or Room (^{o}F)	Range in Hours to Complete Pupal Development
70	84-156
78	60-120
90	48-108

Water immersion tests indicated the pupa could tolerate immersion in water for several hours and still produce a normal adult fly, provided the pupa was removed from the water to a dry surface, but as long as the pupa remained in the water no adults would emerge. Emergence data for the tests reported here are highly variable through 142 hours; thereafter, no eclosion took place. Apparently development of the imago was impeded for the period the pupae remained in water, for after removal, the pupae required about the normal time interval to complete development. It also appeared that if the pupa remained in water for what would be its normal development period, it then succumbed, even though it was removed from the water. Table VIII gives the number of hours pupae were subjected to immersion and the average eclosion obtained after removal.

TABLE VIII

TOLERANCE OF STABLE FLY PUPAE TO IMMERSION IN WATER

Immersion in Hours	Average Eclosion of Pupae	Immersion in Hours	Average Eclosion of Pupae
16½	90	78	78
		93	76
17	40	98	83
18	100	113	10
20	88	117	50
22	100	120	10
24	55	142	40
25	100	160	0
41	55	192	0
44	0	194	0
48	0	215	0

TABLE VIII (continued)

Immersion in Hours	Average Eclosion of Pupae	Immersion in Hours	Average Eclosion of Pupae
72	100	360	0
88	98	000 (control)	75

The primary adult emergence pattern appears to be circadian, but with a secondary peak about halfway between the principal peaks. This same general relationship occurred regardless of the light conditions, but those pupae exposed to outdoor natural conditions emerged in much greater numbers the 2nd and 3rd days than those pupae held in either light or darkness in the laboratory. Furthermore, all the peaks of emergence of the outside pupae were more acute than were those of the inside pupae. Although the peaks for both inside conditions were obvious and occurred at the same time of day as did the peaks of the outside pupae, there was a noticeable trend to broaden or flatten the emergence curve and lengthen the total time emergence required. All primary emergence peaks occurred between 6 a.m. and 9 a.m. and all secondary peaks occurred between 6 p.m. and 9 p.m. The intervals between the peaks usually produced 1 to 10 flies per hour, while peak emergence during day 3, 4, and 5 exceeded 100 flies per hour.

As reported in the paragraph on temperature relationships, the early emerging adults were preponderately males while later the ratio reversed itself. During the 1st 12 hours of emergence the ratio of males to females for total light conditions was 61 to 26; for total darkness, 36 to 15; and for outside conditions, 113 to 47.

The transition of larvae to pupae also brings about a change in

the organism relative to its behavior in liquids. At some point in the physiological changeover the amount of gases trapped within the puparium cause the pupa to float. Although the physiological point was not determined here, the approximate developmental point as a time relationship was established. Some specimens were capable of floating within 2 hours of the time they entered the immobile state although 100% did not do so until 4 hours had elapsed. The following tabulation gives the approximate percent of pupae that were capable of floating at the hours indicated in this test series.

Age in Hours	Percent of Pupae That Float
1	0
2	20
2½	25
3	65
3½	85
4	100

Adults - Fly behavior in the artificial environment of laboratory cages may or may not be indicative of normal stable fly behavior, but does afford the opportunity of watching individuals or small groups in order to gain some insight on the insects activities. Upon first emerging from the pupa, the fly's head protrudes forward greatly as a result of the distended ptilinum and the fly appears generally shrunken or shriveled because the wings are not expanded and the abdomen is not distended. Irrespective of the cage design, the newly emerged fly frantically runs a stop and go, completely unoriented course for 12-28 minutes without giving any noticeable attention to any other personal

activity. This running could be interpreted as an escape mechanism prior to wing development but, I would think the fly would attract much less attention if it would remain quiet.

Finally, the fly chooses a location and remains stationary for a period of 5-11 minutes while the wings slowly unfold and take shape. This appears to occur as a result of flexing and filling of the wing veins. The overall color of the wings at this stage is usually a light grey, but during the following 30 minutes the fly body and wings appear to take on darker hues. Shortly after the wings have been expanded the fly usually grooms or preens the wings by rubbing them above and below with the hind pair of legs. The fly will often walk or move about during this stage, but only for short distances and slowly, rather than the earlier rapid movements. The ptilinum usually begins to recede between 25 to 45 minutes after eclosion and by 45 to 60 minutes the fly has completed the physical change, including distention of the abdomen in females. This latter development does not appear marked for males.

During the first 4 to 6 hours of life following their completion of the physical development process, flies of both sexes were generally inactive in all cages. However, in cages where they had a choice of solid or screen surface, they appeared to prefer the screen. The flies elicited no interest in one another and, in fact, appeared to be anti-social to the point of moving away if another fly came near. They did walk or fly short distances, but most of their time was spent grooming the head with the front legs, the wings with the hind legs, or slowly extending and retracting the proboscis. In the large animal cage their actions were similar to the above, except that the flies divided into general groups - Group I gathered near or on the glass of a recessed

ceiling light, while Group II chose to rest on the dark colored walls of the lower portion of the cage. When a blood saturated pad or a water saturated pad was placed on the screen or within the cages during these first hours the flies failed to demonstrate a marked response. Individual flies did go to the pads, but their nonchalant behavior made it impossible to decide whether they arrived at the pads on purpose or by accident. There were individuals 4 to 6 hours of age, however, that did accept blood when offered on pads. These flies were nearly all males and the quantity of blood taken was small.

During the night the cages were stored in a dark room. There was no indication that the flies were active during this period, but when the lights were turned on in the morning the flies responded for about 30 seconds with a "fright or flight" activity. Shortly thereafter blood or water saturated pads were offered to the 18 hour old flies. The response was now immediate and nearly all flies in the cages began probing the pads and imbibing liquid. The females offered blood, fed to repletion; the males appeared to take a lesser amount. All flies offered water continued to probe for several minutes (5-12) but actually imbibed only a small quantity. When these same flies were offered blood immediately thereafter, they readily accepted the new diet. At first thought, one would think the rapid location of the blood pad by the flies was an olfactory response, and it may well be; however, the flies responded equally well to the water pad, and so, it is possible that both responses were merely reactions to increased humidity. There is also the possibility that positive orientation in the two cages were responses actuated by different receptors entirely.

Beginning on the 3rd day, male flies, when housed in the same cage

with females, began to move about the cage frequently but often returning to the spot of origin. These flies moved in short flights, rarely were they seen to walk. The females continued to be inactive, except to feed periodically. Occasionally, a male would land on a female, but would usually move off again immediately. In one instance, a male was seen to capture a female as she flew across the cage. The two flies fell to the cage floor and the copulatory organ of the male made contact with the ventral tip of the females abdomen. There was a telescoping of the two organs and the insects remained in copula for 4 minutes 10 seconds. After this period of time, the male broke away from the female and flew off. The female remained, more or less, in place for the next 23 minutes. In the large animal cages (rooms) flies appeared to be much more active than in the small laboratory cages and flies of both sexes were seen to fly from place to place more often. However, the habit of males of returning to the spot from which they began a flight was again noticed. It is suggested that males of breeding age may select a "territory" as their domain much like some of the higher animals.

When either sex was housed alone in any of the small laboratory cages the flies demonstrated little activity. In a screen divided cage (Figure 4,B), in which males were placed in one compartment and females in the other, no indication of attraction at the juncture of the two compartments was observed.

The average quantity of blood consumed by 125 individual male or female flies in each of 3 different age groups is given in Table IX. In all tests, the amount consumed when the flies were allowed to feed on a cow was greater than when flies of the same sex fed on blood saturated

cotton or sponge pads. Males always took a smaller blood meal than females of the same age group. In general, as the flies aged, they consumed smaller quantities of blood per meal.

TABLE IX

AVERAGE QUANTITY OF BLOOD CONSUMED BY STABLE FLIES IN MGMS.

Source of Blood	Age of Flies in Days					
	3-5		7-9		11-13	
	Male	Female	Male	Female	Male	Female
Caged cow	10.72	14.64	8.74	11.60	8.70	11.94
Cotton pads	10.32	12.24	7.34	10.14	8.52	8.88
Synthetic sponges	8.12	8.98	8.18	10.74	7.22	8.68

In captivity, under constant temperature conditions, stable flies apparently will feed at any hour of the day blood is offered. In the present tests, blood was offered to unfed flies each hour, on the hour between 8 a m and 4 p m, and in every instance the flies immediately responded to the stimuli and fed. Individually caged flies and groups of 3 or 4 were observed to accept blood twice in one day, 8 am and 4 pm. None were seen to accept more than 2 meals a day.

Table X gives the data relative to survival of stable flies fed (or offered) various substitute diets. A few flies fed bovine plasma or bovine serum survived 22 days. In this particular test, they lived longer than the control flies fed whole blood. It was of interest to observe that a few flies fed only normal saline survived up to 7 days. Flies fed bovine red cells suspended in normal saline laid a total of 4 eggs. One of these eggs hatched, but did not survive. The blood fed controls began laying fertile eggs at 8 days of age. No eggs were

TABLE X

SURVIVAL AND EGG PRODUCTION OF STABLE FLIES FED SUBSTITUTE DIETS

Feeding Time in Days	Flies Remaining Alive on Indicated Day; Number Eggs in (X)							
	Sugar + Water	Red Cells in Saline	Saline Alone	Plasma	Plasma + Saline	Serum	Serum + Saline	Whole Blood
1	250	1089	1139	234	242	255	78	104
2	220	1089	1134	229	224	237	71	97
3	211	1089	819	209	160	224	43	92
4	204	1064	226	152	117	197	36	91
5	159	977	12	128	98	181	30	87
6	85	580	10	117	86	137	28	83
7	46	497	0	111	71	121	24	71
8	0	349(1)		93	9	107	19	69(21)
9		261		77	6	90	16	62(57)
10		141		70	0	87	11	51(27)
11		91(1)		67		77	8	32(15)
12		44(2)		66		64	0	17(33)
13		34		63		53		5(12)
14		0		59		47		0

obtained from flies fed any of the other diets.

Male stable flies demonstrated the willingness and ability to mate with more than 1 female in all tests in which they had receptive females available. In tests where a single male was housed continuously with the same 10 or 20 females, 7 to 11 of the females produced viable eggs, while the other females either died or remained sterile. However, if the male was placed with new lots of 4-day old females, as indicated in the methods section, he mated several of each group of females. Records of 5 males tested in this manner indicate the males inseminated 17, 19, 21, 21, and 23 females. Observations suggest that some females never accept the male and, also, that some female spermathecae examined contained no sperm, even though the female had been seen in copula. Obviously, this indicates all matings do not result in a transfer of sperm. Nevertheless, the present tests demonstrate that males are capable of many more successful matings than has previously been reported.

In these same series of tests, males known to be 13 days old were observed in copula and one 5-day old male was seen to mate with 2 different females with only an interval of 3.5 minutes between the two matings. No specific time of day could be distinguished as preferred for mating, but the constant temperature, constant light conditions may be responsible for this phenomenon.

Females exposed to the attentions of several males were never observed to mate more than once. It is probable that, as Harris et al. (1966) have demonstrated with radioactive tagged sperm, a small number of females do mate a second time, but it is believed most of these matings are females that did not receive sperm transfer on the first

mating.

In studies of the minimum mating age, no fertilization of females was accomplished with males less than 32-40 hours of age and the earliest multiple mating in an 8-hour period occurred when one male was 56-64 hours of age. Mating studies of the female resulted in the same data as for males in regard to earliest mating age. To my knowledge, none of our flies mated at 1 day of age as reported by Killough and McKinstry (1965).

Egg deposition was indicated to be dependent on fertilization. In the 3 replicates of the study to compare egg deposition of mated and unmated flies, it was found that the unmated flies would not normally lay their eggs, although occasionally 1 to 15 nonfertile eggs were found in a cage. Mated flies from the same source produced normal complements of eggs.

Table XI gives average data from 2 tests that attempted to establish a relationship between life expectancy and sex ratio in cages. The data were erratic throughout these tests and, at least, in the context of this study no sex related life expectancy pattern was demonstrated.

As the number of females confined to a cage was increased in number, it was noted that a conflict between flies developed and that physical damage and mortality also increased; this was particularly noticeable in cages 17 through 20 (Table XII). It is believed that these factors strongly influenced the data obtained and therefore the figures presented in Table XII are not a true representation of egg production potential of 17 to 20 flies. However, the figures probably do represent the potential of a crowded community of flies, and the

TABLE XI

LIFE EXPECTANCY OF STABLE FLIES IN CAGES
RELATIVE TO SEX RATIO

Number of:		Average Number Days of Life	
Males	Females	Males	Females
5	-	17.2	-
-	5	-	19.2
1	5	12.0	21.6
2	5	13.5	20.8
3	5	23	27.2
4	5	16.6	22.4
5	5	16.8	14.2
6	5	15.0	13.6
7	5	17.8	20.0
8	5	19.4	16.6
9	5	14.3	13.6
10	5	19.7	16.8
11	5	19.5	11.0
12	5	20.8	18.8
13	5	19.0	11.4
14	5	21.4	20.2

information can be related to the relative inefficiency of crowded mass-colony cages usch as is often observed in insect rearing laboratories.

Besides the apparent effect of crowding, no consistent pattern of egg production was discerned. Flies in the control cages, 5 males and 5 females, deposited an average of 280 eggs; 10 more than any of the test flies.

TABLE XII

AVERAGE EGG DEPOSITION PER FLY RELATIVE TO NUMBER OF FLIES IN THE CAGE

Number of Females/Cage	Average Number Eggs/Female	Number of Females/Cage	Average Number Eggs/Female
1	139	11	215
2	270	12	252
3	237	13	163
4	219	14	210
5	219	15	128
6	169	16	185
7	172	17	96
8	154	18	82
9	264	19	108
10	190	20	97
Control (5 females + 5 males)	280		

Table XIII gives a typical 6 X 6 Latin Square presentation of data from which the attractiveness of the different colors, the importance of position in the room, and the variation among replicates was estimated.

In an analysis of the data, the calculated F values for replicates and treatments (colors) both exceeded the tabulated F value at the 5% level. However, there was no indication that any significant difference occurred due to location in the room. Again, at the 5% level, computation of the least significant difference between colors gave a figure of 35.88. On this basis, brown, white, green, and red attracted significantly more flies than blue, but there was no apparent difference between any other combination.

An average of about 11.1% of the flies released were found to be on the colored boards at any one time, the remainder chose to rest on the walls or screening of the large animal room. The results and conclusions are based on only those flies that were counted on the boards.

Field Studies

Kerr County Survey - Visual observations for the presence and abundance of stable flies in Kerr County in 1964 and 1965 established that the fly is not numerous throughout the county on range or pasture animals. When cattle were on dry-land or hill pastures, which are estimated to comprise 95% of the county, not a single stable fly was observed to attack any animal at any time of the year. The presence of stable flies in the county was invariably associated with the activities of man and, in particular, dairy situations. However, there was not a farmstead, dude ranch, or other animal related property at which a few stable flies could not be found in the vicinity of the ranch headquarter buildings in August or September. The greatest number of flies were located at dairies and barn-lot cattle farms situated along or near the Guadalupe River between Center Point and Kerrville, except that in the immediate vicinity of the biting fly laboratory an

TABLE XIII

AVERAGE NUMBER OF STABLE FLIES ATTRACTED TO AND RESTING ON BOARDS OF DIFFERENT COLORS[1]

Test Replicates	Location of Board in Room						Row Totals	
	1	2	3	4	5	6	ΣX	ΣX^2
1	153(A)[2]	59(B)	120(C)	152(D)	126(E)	147(F)	757	101,879
2	97(F)	78(A)	66(B)	115(C)	98(D)	125(E)	579	58,303
3	115(E)	104(F)	86(A)	63(B)	107(C)	61(D)	536	50,576
4	50(D)	68(E)	80(F)	127(A)	59(B)	90(C)	474	41,234
5	181(C)	113(D)	255(E)	165(F)	193(A)	119(B)	1026	189,190
6	68(B)	132(C)	124(D)	99(E)	138(F)	78(A)	639	72,353
ΣX	664	554	731	721	721	620	4011	--
ΣX^2	85,928	55,198	112,953	93,453	96,703	69,300	--	513,535

[1]Calculated F values: for treatments = 3.88, for replicates = 8.99, and for location = 1.22. Tabulated 5% F value for 5 and 20 degrees of freedom = 2.71.

[2]A = red; B = blue; C = white; D = black; E = brown; and F = green.

abnormal number of flies was present due to the stable fly rearing facility. Small numbers of stable flies were present throughout the summer--May to September--in the picnic area of Louise Hays Park, but none were ever seen at the Kerrville sewage disposal plant or city dump ground. An unusual situation involving 10 bison was located near Hunt, Texas. These animals were fed hay daily in one location and a small (50 X 50 ft) area of debris developed that was made up of waste hay, feces and urine. In this debris, stable fly larvae were commonly found and adults in numbers of 5 to 7 were often seen on the bison. Apparently the bison were not seriously disturbed by the feeding flies as they made no real effort to dislodge them.

In both years, stable flies began to increase in numbers in mid-March, slowly developed a moderate density (average 3-5 on dairy cows) by the 1st of June, remained static or slightly decreased until early August, and then increased to densities of 8-12 per dairy cow in mid-August, through September, and early October. The numbers decreased to negligible numbers in November, but all through the winter an occasional fly could be found on bright sunny days at a dairy near Kerrville. At this same situation and at another dairy near Mooney Aircraft, 3rd instar larva could be found in the barnyard debris every month of the year.

Stable fly density, except for the dairies and at the experimental station, rarely exceeded a count of 2/head on cattle or horses in the county, although in late August 1964 and early September, following several days of rain, the number of adult flies increased throughout the county by an average factor of 2X to 3X for approximately 3 weeks. Figures 7 and 8 present typical daylight hours temperature and feeding activity curves for early July (2nd) and late August (27th) as recorded

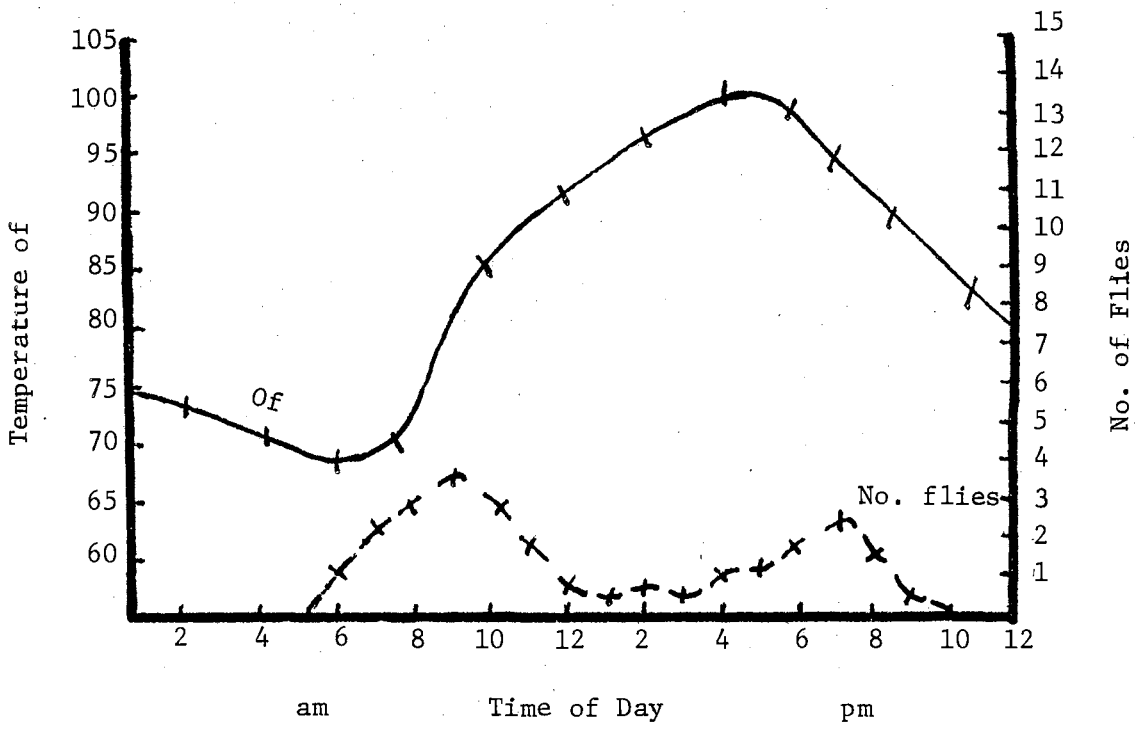

Figure 7. Temperature and Stable Fly Feeding for July 2, 1964

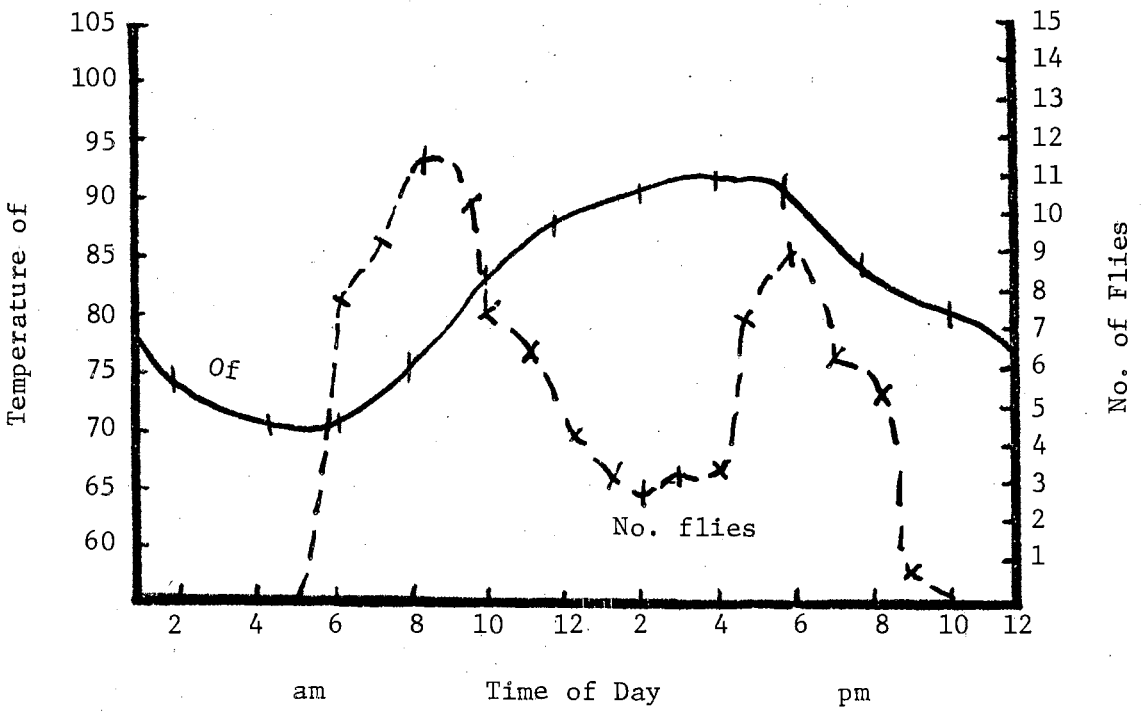

Figure 8. Temperature and Stable Fly Feeding for August 27, 1964.

at dairy L near Kerrville. The general pattern of the feeding activity is similar but the numbers of flies active are much less in the July count.

Thus, it was established that Stomoxys were found in discernable numbers in Kerr County only in locations where moisture and organic debris was available for larval development and, at least, periodically suitable hosts were present to provide blood needs for adults. Even though general distribution was not observed, the flies must commonly travel considerable distances by flight or on a vehicle or animals to be established in each suitable environmental niche in the county.

In suitable environmental locations, such as the dairies, stable flies are found resting on dead twigs on live oak, oak, and cedar trees at elevations of 6-12 feet above the ground during the day. Twigs of 1/8 to 1/4 inch in diameter appear to be preferred and the flies invariably rest parallel to the long axis of the twig. Trees situated near water tanks, ponds, or other sources of moisture appear to be preferred. Stable flies have also been found resting on board and wire fences, the inner and outer walls of milking parlors, the sides and edges of metal stock tanks, on inner and outer walls of wooden sheds, and, for short periods, on the ground. In the morning until 9 to 10 am they will usually select a sunny location but during the remainder of a clear, warm or hot day they appear to select shaded resting locations. On bright days, broken by an occasional cloud, the flies often become momentarily active during the time the sun is hidden. Flies were rarely seen to assume what could be interpreted as a resting state when they were on cattle. Apparently, they came to cattle or other animals only to satisfy their hunger. Resting position bore no relation to compass

direction, but did relate to the long axis of the small objects on which they landed. No indication of a gregarious attitude was evident during the daylight hours, except when females located a particuarly acceptable egg laying medium then several would often select the same localized spot to deposit eggs. This action was interpreted as an external stimulus for oviposition and not related to any desire to associate with their fellow flies.

Between 6:30 and 8:00 pm, during the summer months, Stomoxys seek a night resting location. Often this is the oak trees as described for day time resting sites, but increased numbers are found within open shed or outbuildings resting on ceiling rafters, electrical or other wires, or on isolated supporting timbers. Once located for the night, the flies are not easily disturbed. It was possible to pick up the fly or touch it without apparent alarm. During the daylight hours the flies readily moved when approached, unless they had recently fed. Fully distended females were particularly lethargic.

Field Study Observations - The observations reported for biology and behavior of the stable fly in the field were primarily recorded at the L dairy, but certain other notes of interest related to horses, mules, and miscellaneous sources are also included. In Kerr County, stable flies were observed to take blood from cattle, horses, mules, bison, a dog, and a pet deer. On horses, cattle, and mules the flies obviously preferred to feed on the lower front legs (Figure 9) although a few did feed elsewhere. Actually flies often alighted on some portion of the body first, and then moved to the front legs after being disturbed. At times when the lower legs were soiled with mud or manure, the flies fed above the soiled area of the legs.

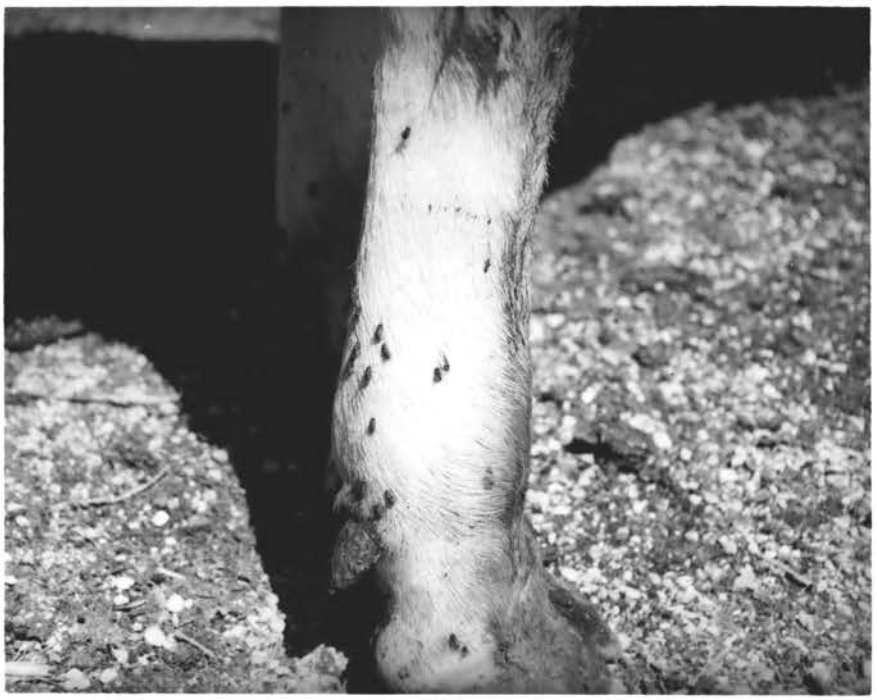

Figure 9. Stable Flies Feeding on Fore Leg of Cow.

Feeding occurred to some extent all through the day especially in March and April, but in the warmer months peak feeding activity centered around 7-8 am and 6-7 pm. At air temperatures above 90 F, the flies activity was considerably reduced in sunlit situations, even though an animal in a shady location was still being attacked.

Hungry stable flies were closely observed while they proceeded through the feeding process. A fly would land, move its feet about a few times as if aligning the animals hair, extend the proboscis downward to a near-vertical position, press the proboscis downward into the wound, and begin to make expansion and contraction movements. As the blood began to enter the abdomen drops of fluid were expressed from the anus. Often the fly would be disturbed in mid-meal and would move to a new location and repeat the process. Specimens that completed blood meals, did so in as little as 2 minutes 16 seconds and as much as 6 minutes 40 seconds. Males rarely fed enough to distend the abdomen.

Nearly all cattle or horses would actively fight off the attacking stable flies, but the before mentioned bison and especially donkeys and mules seem to ignore the feeding flies.

In a 4 day period 202 Stomoxys were captured off of a burro to obtain an estimate of the sex ratio of feeding flies. Females predominated with 69.6% of the total; males were never present at more than 45% of any one collection.

Between the hours of 7 am and 9:30 am males were commonly seen perched on twigs or branches about 6-8 feet above the ground. From these vantage points they would make short, darting flights to another twig or just into space, then would return to the point of origin. This behavior would be repeated from a few seconds to 2 or 3 minutes

later. If a house fly or stable fly of either sex ventured into the immediate area, one or more males would dart out to intercept the newcomer. On one occasion a male was seen to capture the female in flight and the two joined in copula and fell to the ground. They remained in copula for approximately 4 minutes. After breaking off the union, the male flew back to his perch in the tree, while the female remained in the same spot on the ground for about 20 minutes.

Ovipositing females were observed laying eggs in wet straw that was mixed with calf manure. These flies would crawl about and between the layers of straw and place 1 to as many as 25 eggs in one spot. They always seemed to attach the eggs to a wet piece of straw. Some of the eggs were collected, as indicated in the methods section, and at a varying ambient temperature of 66 to 97 F the first egg hatched in 29.5 hours and 84% had hatched within 32 hours.

Larvae of Stomoxys were found in Kerr County in cow pats, cow manure and hay around feed bunks, wet donkey manure, wet horse manure and hay, hay and wet dirt by water tanks, calf manure and hay, and wet debris in a horse corral. Specimens reared from these various larval situations varied greatly in size. In general, those originating from isolated horse or cattle droppings were smaller flies than those originating from hay, or hay and manure mixtures.

One batch of eggs was placed in wet donkey manure immediately after being laid and was returned to the immediate environment from which it was collected. Temperature of this wet manure reached a maximum of 100 F during the development of the larvae and the larvae did not leave the medium. The larvae pupated after 6 days and the adults emerged 3 and 4 days later, completing an egg to adult cycle in 9 to 10 days.

SUMMARY AND CONCLUSIONS

A review of the literature relating to Stomoxys calcitrans (Linnaeus) provides a background of information on the economic importance, the distribution and abundance, the life history, the biology and behavior, the recognition characters, and the history of control efforts of this blood-feeding muscoid.

All of the laboratory portions of this study were conducted in the facilities of the United States Department of Agriculture, Biting Fly Laboratory, Kerrville, Texas, with equipment and conditions devised specifically for biting fly research. The Kerrville laboratory strain of S. calcitrans was used as the test insect. Laboratory holding and experimental cages were custom made of plastic and paper cartons in various sizes to fit the need of the specific purpose and 9 X 10 X 18 ft large animal rooms were used to hold cattle during insect feeding tests and for fly resting site tests.

Various tests were completed on each stage of the life cycle. Consideration was given to the numbers of eggs deposited, the percentage hatch, and the time interval of the egg stage. Resistance of the egg to drying and to submersion in water were also studied.

Projects with larvae determined the length of the larval stage at 3 temperatures, the effect of crowding, the moisture requirements, and the tolerance of larvae to submersion in water. The length of the pupal stage at 3 temperatures, the effect of water immersion, and the eclosion pattern of adults from pupae were investigated. The point in time when

forming pupae first float was approximately established.

General behavioral patterns for Stomoxys adults were observed while the flies were confined in plastic cages and when in large animal rooms. Feeding characteristics and tests of diets other than whole blood were investigated. Mating activity studies of both sexes considered mating age, number of matings, time of day preferred, time interval between matings, and the time in copula. The effect of various numbers of female flies housed in a specified size of enclosure on egg production and the longevity of adults relative to the sex ratio of flies confined in a given space were also considered. Attraction of adult flies to various colors when the flies were seeking resting sites was investigated by releasing flies into a large animal room which contained painted wood strips.

Field biology and behavior observations were recorded in Kerr County, Texas, during 1964-65 for all seasons of the year, but mainly for the period of April through October. The county's general ecological and climatic conditions are described, as well as, typical Stomoxys habitats. Cursory surveys were conducted periodically throughout the county to establish the general presence and abundance of flies and 21 potential or actual stable fly habitats were selected for more intense study.

Stable fly biology and behavior was determined among wild flies by close visual observation of the activities of adult flies throughout the day and under various weather conditions. Feeding, resting, mating, and egg laying habits for the area were recorded. Egg and larva studies were accomplished by collecting eggs immediately after females laid them and observing egg hatching and by rearing larvae in natural mediums.

At room temperature in the laboratory most females laid their first eggs on the 7th or 8th day after eclosion from the pupa and usually laid some eggs on 5 or 6 out of the first 7 days once they began laying. Egg production of females varied from 22 to 307, with an average of 183. One fly laid periodically through 31 days. Egg hatch averaged 79.95% in these tests. Eclosion of the larva from the egg at 78 F $\pm$ 2° and relative humidities of 50% or 80% exhibited low survival rates. Submersion of eggs in water delays the time required to hatch and reduces the total hatch obtained, but some eggs remained submerged for at least 4½ hours and the embryos survived.

Development of larvae from eclosion of the egg to pupation required 336-384, 240-264, and 216-240 hrs at constant temperatures of 70, 78, and 90 F, respectively. Crowding, or over-population, of larvae in medium produced smaller and fewer pupae as the numbers of larvae were increased above approximately 3 per gram of CSMA medium. Larvae with ample food and living space produced pupae weighing in excess of 14.7 mgms each, while medium containing 10 larvae per gram produced small pupae with an average weight of 8.6 mgms. Larvae survived and developed to maturity in mediums of widely varying moisture content. A rather consistent pupa size and percentage formed occurred in mediums having CSMA-water ratios varying from 30:20 to 30:180. Third instar larvae that withstood submersion in water for up to 17¼ hrs still produced 79% pupae and 58% of the pupae produced adults. It would appear the larval stage is highly tolerant of water and this ability is probably a valuable survival characteristic should the organisms habitat be subjected to flooding.

Pupae held at constant temperatures of 70, 78, and 90 F required

between 84-156, 60-120, and 48-108 hrs, respectively, to complete development. The first flies to emerge at all temperatures were preponderately males. Water immersion data for pupae were highly variable but did indicate some pupae could be in water for up to 142 hrs and still produced adults. However, the pupae had to be removed to a dry surface in order for eclosion to take place. Thus, it was demonstrated the pupal stage could survive water immersion for several hours and therefore survive a temporary flooding of the pupation site; however, continuous flooding for a period of 7 or 8 days would destroy most of the pupae and might be considered as a control measure under special conditions.

The eclosion or emergence pattern of the adult from the pupa was demonstrated to be circadian, but with a secondary peak midway between the principal peaks. The primary peaks occurred between 6 am and 9 am regardless of light or temperature of the environment. Conversion of a larva to a pupa required from 2 to 4 hours for the insect to progress from the beginning of the immobile state to the physiological-morphological state where the organism would first float in water.

The behavior of emerging flies in the laboratory and in nature proved to be similar and essentially as other authors have described. During the first 4 to 6 hours of adult life, stable flies exhibited little interest in feeding and most of those flies that did accept food were males that took only small quantities. However, after a period of 18 hours had elapsed flies offered any of several liquid diets readily fed. As flies responded as quickly to water saturated pads as they did to blood pads, the question arises as to whether the feeding response was olfactory or a response to increased humidity.

Males generally began to demonstate sexual aggressiveness when 3

days of age and in laboratory cages or outdoors would move about in short flights that generally terminated at the point of origin. Those successful matings observed resulted from males "capturing" females in flight and a subsequent alighting on the ground or other surface where copulation was completed in about 4 minutes. Individual flies housed in small cages demonstrated little activity of any kind.

Average blood consumption by males was less than that of females of the same age and, in general, as flies of either sex aged they consumed progressively less blood. The tests indicated males consumed from 7.34 to 10.72 mgms/fly, while females consumed from 8.68 to 14.64 mgms/fly. Flies held under colony conditions would feed at any hour of the day but probably not over twice in one day.

Stable flies fed various substitute diets survived for 6 to 22 days but only those flies fed whole blood produced eggs that survived. Flies fed blood plasma or serum lived as long as those receiving whole blood and 4 eggs were laid by flies fed on normal saline containing washed red blood cells. A few flies lived up to 6 days on normal saline alone.

Male stable flies demonstrated the ability to mate with up to 23 females but no female was observed to mate more than once. It would appear that the female is normally a monogamous insect. Minimum mating age for both males and females was determined to be when the flies were between 32 and 40 hours old. Eggs were not ordinarily deposited by the female unless she had been fertilized and thus most virgin females retained their eggs until death.

Tests to establish the effect of sex ratio on survival of caged flies were inconclusive, as were tests to determine the influence of confining together varying numbers of females on egg production. In the

latter tests, mortality increased as crowding became more acute.

Preliminary tests to establish color attractiveness to resting stable flies indicated that brown, white, green, and red were more attractive as resting surfaces than blue. Or perhaps one might consider blue repellent to the flies. It was also indicated that differences between replicates was significant but that location within the test room was not.

Field studies in Kerr County established that the stable fly was abundant only in very localized situations. The situations of primary importance were all dairy farms, but moderate numbers of flies were also found at dude ranches, summer camps, horse ranches, a bison ranch, and near the United States Department of Agriculture's Biting Fly Laboratory. In general, the semi-arid environment is not one that supports an abundant Stomoxys population. The seasonal population trend as observed feeding on cattle at a dairy ranch indicated the first adult flies to be active in mid-March. By early June, 3 to 5 flies were counted/cow and in mid to late-August the numbers increased to 8 to 12/cow. The increase of flies appeared to correlate with increased moisture conditions. In nature, flies were observed to feed throughout the day but the greatest numbers were on the cows before 10 am and after 4 pm.

In suitable environmental locations flies were often found resting on twigs in trees at elevations of 6-12 ft above the ground and invariably the flies rested parallel to the long axis of the twig. Males often utilized such locations, especially to fly out and capture passing females. Flies were observed on cattle only when seeking food; apparently the flies do not rest on the cattle. Also, the flies do not appear to be gregarious in nature as they are rarely seen closely asso-

ciated in any numbers.

Stable flies were seen to feed on cattle, horses, mules, burros, bison, a dog, and a pet deer in Kerr County and, except for the dog, the feeding location selected was usually the lower front legs. Observations of the feeding act indicated it to be essentially as described by other authors. Of 202 flies captured feeding on a burro, 69.6% were females and captured males never exceeded 45% of any collection.

In Kerr County, stable fly larvae were recovered from cow pats, cow manure and hay mixtures, wet donkey manure, wet horse manure and hay mixtures, hay and wet soil, calf manure and hay, and wet debris in a horse corral.

Although not a major pest species, the stable fly has been shown to live in the semi-arid region of central Texas and was indicated to be locally abundant under moist conditions when associated with animal manure or decaying organic matter. Chemical control of the fly is probably not warranted, but increased attention to sanitation in the offending restricted locations would, no doubt, alleviate the occasional serious problem that occurs.

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