The courtship behavior of the house fly, Musca domestica L., and face fly, Musca autumnalis De Geer: with notes on the experimental hybridization of the two species.

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THE COURTSHIP BEHAVIOR OF THE HOUSE FLY, *MUSCA DOMESTICA* L.,
AND THE FACE FLY, *MUSCA AUTUMNALIS* DE GEER, WITH NOTES ON
THE EXPERIMENTAL HYBRIDIZATION OF THE TWO SPECIES

A Thesis Presented

By

EDWARD N. TOBIN

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THE COURTSHIP BEHAVIOR OF THE HOUSE FLY, MUSCA DOMESTICA L.,
AND THE FACE FLY, MUSCA AUTUMNALIS DE GEER, WITH NOTES ON
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January, 1972
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I. INTRODUCTION


The mating of flies has, no doubt, been a common sight to men for centuries. Indeed, so common as to have been mentioned by Shakespeare in *King Lear*, "And the small gilded fly does lecher in my sight. Let copulation thrive!" (cf. West, 1951). Despite the frequency of observation of this act in flies, little attention has been given to the courtship behavior of the ubiquitous house fly, *Musca domestica* L.

Some observations on the mating habits of the house fly have been recorded by Berlese (1902), Hammer (1941), Hewitt (1914), Réaumur (1738), and West (1951). More recently, Chang (1965), Murvosh, et al. (1964a), Rivosecchi (1958), and Soliman, et al. (1968) have mentioned house fly mating behavior. The observations of these authors were not centered on the behavioral aspects of the mating of the flies, rather, they were economically oriented. Since the behavior is extremely fast and resembles struggling, their descriptions are inaccurate or incomplete. The present study was conducted employing motion pictures, and frame by frame analysis; thus the activities could be viewed in detail.

The face fly, *Musca autumnalis* De Geer, a recently introduced pest to North America, has been somewhat neglected by North American scientists where mating behavior is concerned. Hammer (1941) and Teskey (1960) reported field observations on the mating habits of this fly. Lohda, et al. (1970) and Teskey (1969) attempted to describe the courtship behavior of this species, but were only partially successful due
to the speed and complexity of the courtship elements.

A complete description and analysis of the behavioral patterns involved in the courtship of these two species will open many avenues for further investigations regarding the physiology, genetics, phylogenetic relationship and evolution of behavior in the genus Musca. As will be seen in the next section, behavior and behavioral patterns can be extremely useful tools for other biological disciplines, while these other fields of study also aid in explaining behavior.

B. The Importance of Behavioral Studies

One aspect of behavior may be defined as, "Externally directed movements of an intact animal." Using this definition, we are all students of behavior, since we watch animals and their movements daily. Almost everyone watches the behavior of dogs, cats, birds, fish, people, etc. From naive curiosity one begins to ask questions as to the cause or importance of certain types of behavior of animals.

In addition to providing new information about the habits and activities of animals, which is often extremely interesting, the study of behavior yields information applicable to other fields. Such information is often unexpected at the outset, but one can expect certain information regarding the physiology, ecology and systematics of the species involved. In addition, practical applications, such as using behavioral patterns and habits in the control programs of insect pests, are of interest to farmers, pest control operators, medical entomologists, etc.

In the field of physiology behavior is a very valuable tool, for
behavior is the manifestation of physiological phenomena. Evans and Dethier (1957) have used behavior in their analysis of the neurophysiological basis of feeding in Phormia regina (Meigen). The visual acuity of honeybees was studied by Hertz (1935) using behavioral patterns. Many other analyses of physiological phenomena involving pheromones, food preferences, endocrinology, etc., of insects are based on behavioral patterns.

The study of phylogenetic relationships between species may be clarified by behavioral evidence. An example of this is the case of sibling species of Drosophila (Dobzhansky, 1946). In this vein, the evolution of behavior is, at least in some cases, correlated with morphological evolution as shown by studies on Drosophila mutants (Bastock, 1956). Finally, regarding evolution and phylogeny, courtship behavior may be one of the isolating mechanisms preventing hybridization and speciation.

In the field of ecology, differences in niches between species is interrelated with behavioral patterns. Also, the effect of overcrowding within a population may have behavioral manifestations such as cannibalism, aggression, etc. (Calhoun, 1962).

Attractants such as pheromones, and some baits are used with traps in controlling insect pests. These attractants and baits are based on the behavioral patterns of these pest insects. Knowing the mating habits of pest species has enabled entomologists to utilize chemosterilization and radiation sterilization to control certain pests.

Descriptive studies of stereotyped behavioral patterns serve as a basis for studies of other aspects of behavior. Examples of this are
the study of releasers, typical intensity and motivational basis of behavior. From the above examples one can see the complex interrelationships of all aspects of an animal's biology. A basic step in uncovering these interrelationships is a descriptive study and analysis of behavioral patterns.

C. Objectives of the Research

The primary objective of these investigations is to gain a better understanding of the biology of the two species involved, through a comparative and descriptive analysis of their courtship ritual and mating behavior. Another objective is to attempt to hybridize them in the laboratory.

The third objective is to obtain a basis for further behavioral studies regarding the mating behavior of face fly and house fly.

D. Problems Investigated

The two major problems investigated were attempted hybridization between house fly and face fly, and a comparative and descriptive analysis of the courtship ritual and mating behavior of these two species.

The hybridization experiments were designed to determine whether or not the two species would mate and produce hybrids. They mated but did not produce hybrids, thus the investigations were centered on the barriers to hybridization which are effective in separating house fly and face fly. Sperm transfer, fertility of eggs, and viability of zygotes were investigated.
The descriptive analysis of the courtship ritual of these two closely related species of flies was undertaken to show the components of their courtships and reveal possible functions for each component. Some observations on the degree of epigamic recognition and homosexual activities are mentioned to shed further light on the mating behavior of these flies.

Finally, a comparative study of the courtship of these species was made to show differences and similarities between their mating behavior in hope of adding to the knowledge of the evolution of their behavior to see how it compares with the present phylogenetic scheme for the genus Musca.
II. MATERIALS AND METHODS

A. Maintaining and Rearing Stock Colonies

1. Rearing house flies. The house flies were from a colony of the Orlando Regular strain and were reared in the laboratory for approximately two years.

The colonies were maintained in a rearing room with no outside light source, i.e. windows were blocked and insulated. Three banks of eight foot I.T.T. F96 T12/CW, white fluorescent bulbs were used as a light source. Each bank consisted of two bulbs and was placed at the middle of a row of cages. The photoperiod was maintained at 16 hours light and 8 hours dark by an automatic timer. Temperature (27± 3°C) was controlled by a combination of an Arvin electric space heater and a Westinghouse air conditioner. Humidity (50± 5% R.H.) was controlled with a West Bend automatic humidifier.

Adult flies were kept in wooden frame cages covered with plastic screening and fitted, in the front, with eight inch wide tubular Orthopedic Stockinet. The stockinet provided a tunnel-like opening which permitted access into the cage without any flies escaping. The cages were approximately 53 X 60 X 60 cm, with the opening for the stockinet approximately 25 X 25 cm. They were kept on metal racks approximately 15 cm, from the bulbs.

A constant supply of food and water was available to the adults. The food was nonfat dry milk and granulated sugar, placed in separate seven ounce Dixie food dishes. Several dishes were placed in each cage.
Water was supplied by a square plastic container 10 x 10 x 8 cm, with a tight fitting top. Wicks made from Absorbal dental gauze were fitted through holes in the top and extended into the water. The only other source of nutrients was Maltsupex, a barley malt extract, which was provided once a month, or when increased egg production was necessary. Food and water were replaced at least once per week, at which time dead flies and spilled food were removed from the cages. Fresh, clean cages with new flies were started at three month intervals to minimize the effects of inbreeding and to prevent diseases.

Fresh, rectally collected bovine feces were placed to a depth of 7.5 cm, in round plastic dishes 9.5 cm, high and 16.5 cm, in diameter. These oviposition dishes were placed in the cage with the adults every other day. They were removed when fresh manure was added, except on Friday, when no manure was placed in the cage. The manure removed from the cage was examined for day old larvae, and some manure and larvae were placed in an enameled pan containing more manure for development.

The container for the larvae consisted of a white enamel pan 22 x 39 x 11 cm, filled 5 cm, high with fresh bovine feces three quarters of its length. The remaining one quarter was filled with sifted sand to allow an area for the larvae to pupate. The pans were covered with a double layer of cheesecloth held in place by an arrangement of twine and elastic rubber bands. These pans were left on shelves in the rearing room until pupation.

After five to seven days in the enameled pans, the sand was removed and sifted and the pupae removed. The pupae were placed in clear
plastic cylinders 13 cm. high and 13.5 cm. in diameter. These containers were fitted with tightly fitting tops. A circle 10 cm. in diameter was cut out of the top, and plastic screening glued to cover it. When the first adults emerged from a batch of pupae, the container was placed in the cage with the adults and opened to allow the adults access to the cage.

2. Rearing face flies. Face flies were collected from a field in western Massachusetts, and reared in the laboratory for approximately two years. The rearing procedures for face fly were identical to those used for the house fly.

The problem of mixing the colonies was easily resolved between these two species. The puparium of face fly is white, while that of the house fly is brown.

B. Experimental Procedures

1. Separating sexes and maintaining the experimental flies. Several methods for separating male and female flies were tried. The most satisfactory method was found to be isolation of pupae in shell vials. One pupa was placed in each vial, which was then covered with a cork stopper. The vials were separated, by species, and placed in two holders, each of which held 100 vials. Thus, approximately 50 males and 50 females were available for each species. As the flies emerged, the sex was determined and they were placed in cages marked with species, sex and date of emergence.

The cages for holding the same sex of a species were constructed from the plastic containers used to hold stock pupae. These containers
were fitted with stockinet held in place and held closed by rubber bands. Sugar, milk and water with Absorbal\textsuperscript{®} wicks were placed in separate Peel-a-Way\textsuperscript{®} tissue embedding molds, 3 X 2.5 X 2 cm., and left in the cage.

These cages were left in a Sub-Zero\textsuperscript{®} control chamber at 27°C., 16 hours light and 8 hours dark. Humidity was not controlled.

The criteria for determining the sex of the flies were the external signs of sexual dimorphism. Female flies, of both species, are characterized by a wide space between the compound eyes, and a uniformly grey abdomen. The males, on the other hand, have compound eyes almost touching in the middle, and an abdomen with a median dark stripe, surrounded by light areas, ending in a darkened area at the posterior tip of the abdomen.

Determination of species was uncomplicated. Since the pupae were isolated, the species was determined by the color of the puparium.

2. Intraspecific matings. Virgin insects of the desired age were caught in the holding cages with shell vials and transferred to the observation cage. The observation cages were identical to the holding cages, but lacked food and water. The insects were never anesthetized with carbon dioxide prior to the experiments.

3. Interspecific matings. Virgin insects of the desired age, sex and species were removed from the holding cages and transferred to a wooden frame cage which was a miniature of the rearing cages (25.5 X 25.5 X 25.5 cm.).

Various proportions of males and females were used, as will be discussed later.
The cages were provided with powdered milk, granulated sugar and water in the same way as the stock cultures. These experiments were conducted in a sub-Zero control cabinet, maintained at 27°C, 16 hours light and 8 hours dark.

Manure was provided every day in Dixie food cups. Strict pre-cautions were taken to prevent contamination of the manure by mites or other flies. For example, the bucket was covered immediately after the manure was collected; the buckets were under constant surveillance; manure for the experiments was taken from the middle of the bucket and placed directly into the cages.

The manure was removed after 24 hours and examined for eggs under a dissecting microscope at 10 to 60 magnification. Then it was placed in a plastic container, of the type used to hold stock pupae and covered with a tightly fitting cover. After another 24 hours the manure was examined for empty eggs cases or newly hatched larvae under the dissecting microscope. Several eggs were removed to determine developmental stages of the embryo. The eggs were dissected in insect saline under a microscope at 60 X, and the embryonic condition, if any, was noted. Finally, the manure was examined for larvae by mixing it with water and examining the mixture under a microscope. After two days the larvae were large enough to see without a microscope.

4. Homosexual behavior. Homosexual activities were observed through the holding cages where flies were of the same sex, species and age.

5. Sexual behavior studies. The studies of intraspecific and interspecific mating behavior, and homosexual activities were all conducted in the observation cages previously described. The preliminary
observations, to determine if the two species did have a courtship ritual, were done without the aid of magnifiers. Since the flies are small and the activity extremely fast, a Dazor circline magnifier, model M-1408 was used. The magnifier proved unsatisfactory, for the movement of the flies was too fast to be accurately determined. For this reason, slow motion photography of the mating was used to analyze the courtships. The photographic technique will be discussed in a later section.

Counting mating attempts during a given time and timing pseudo-copula in homosexual studies was accomplished using a Veeder counter and a Fisher stopwatch.

6. Dissections. Females from both intra- and interspecific crosses were dissected to determine the presence of sperm in the spermathecae. The females were anesthetized with carbon dioxide and decapitated. The dissections were carried out in insect saline under a Wild dissecting microscope at 10X. The abdomen was squeezed and the extruded ovipositor grasped at the tip. Gentle pulling removed the oviduct and spermathecae. Extraneous material was removed and the spermathecae were placed in a drop of saline and covered with a cover slip. The slide was viewed under a Wild phase-contrast microscope after the spermathecae were crushed. Sperm, when present, were usually obvious under lower power (100X), but occasionally oil emersion was necessary.

The remainder of the abdomen was opened up and the ovaries were examined for stage of development.

The insect saline used in the dissections was Brelar's saline, and was composed of six grams of sodium chloride, .2 grams of potassium
chloride, .2 grams of calcium chloride, and .2 grams of sodium bicarbonate, and one liter of distilled water (Breland, 1961).

Photographic techniques. The arenas used for the photography were similar to the observation cages. The only differences were that the cages used for the photography had \( \frac{1}{2} \) inch of paraffin covering the bottom, and had a hole in one side. Melted paraffin was poured into the cage and allowed to cool. A hole to fit the mouth of a shell vial was drilled in the side of the cage. This hole was fitted with a vial to prevent the escape of the flies, and to introduce the males into the arena.

A virgin female fly was anesthetized with carbon dioxide and pinned with an insect pin. The pin was placed off center through the thorax. The female was pinned to the wax bottom of the cage, and the pin was cut level with the thorax. Care was taken to insure that the female was able to move all appendages and that the legs touched the paraffin. Once the female was in place, the sleeving of the cage was closed. Males were then caught in shell vials. The vials were covered and set aside until the female recovered from the carbon dioxide.

The lights used to illuminate the flies were one Chadwick high intensity lamp and one Bausch and Lomb microscope lamp, model number 31-33-53. These light sources were selected because conventional photographic lights produce too much heat and kill the insects. Also, fluorescent lights were unsatisfactory because the light from them is not measured correctly by the automatic light meter of the camera. The two lamps were arranged to illuminate the female as much as possible. At this point the lights were turned off and the camera was made ready for
filming.

The camera used in this study was a Beaulieu® R 16 movie camera, powered by a Beaulieu® 500 milliamp nickel-cadmium battery. The camera was mounted on an Elevator Husky IV® tripod. In order to get close-up movies of the flies, a Zoomar® makro-kilar 2,8/90 lens and 15mm Beaulieu® makro-zwischenring extension tubes were used. The focusing apparatus of the camera was corrected to the operator's vision, so that when the image appeared in focus to the operator, it was in focus on the film. The camera was equipped with a built-in light meter.

The film was taken at 64 frames per second, using Kodak® 4X reversal film (ASA 320). After setting the camera to the proper filming speed and ASA setting, the camera was focused on the female and the light meter was checked to insure proper illumination. When the camera and female were ready to begin filming, a vial of males was selected and placed in the hole in the side of the cage. When the males left the vial, it was removed, and the hole in the cage was closed with a cork. The mating strikes of the males were filmed.

The exposed film was processed and viewed. Using a 16mm projector was unsatisfactory, because the movements of the flies were too fast to observe accurately. A 16mm Craig® editor-viewer was utilized to view the films, frame by frame. Recording the description of the films' contents was accomplished using a Norelco® Carry Corder 150 tape recorder and a Norelco® FP-86A foot pedal. The recordings were played back and transcribed. Timing the various elements of the courtship was accomplished by counting the number of frames of a sequence in which the element occurred. Since the filming speed was 64 frames per second, each
frame represented 1/64 seconds.
III. LITERATURE REVIEW

A. House Fly and Face Fly as Livestock and Household Pests

1. House fly. According to West (1951) and many other authors, house fly has been a nuisance to man throughout recorded history. Since it is a pest by its mere presence, and is a potential vector of many diseases and parasites, the house fly and its biology have been the subject of innumerable articles and several books (Graham-Smith, 1913; Greenberg, 1971; Hewitt, 1914; Howard, 1911; West, 1951).

House fly, when found inside dairy barns, is not considered a pest of livestock, as are horn fly or face fly, but rather a nuisance to man and domestic animals in general (Anon., 1969). The irritation caused by the house fly is a subjective matter; however, its relationships with pathogenic micro-organisms, nematode and helminth parasites has been demonstrated (see Greenberg, 1971).

Greenberg (1971) lists the numerous organisms that have been associated with house fly. Among the more notorious of these are: Polio virus, Pasteurella pestis, Brucella abortis, Bacillus anthracis, Mycobacterium leprae, Mycobacterium tuberculosis, several trypanosomes, Trichomonas hominis, Trichomonas foetus, Hymenolepus species, Ancylostoma species, and Ascaris species.

2. Face fly. Since the first report of face fly in North America (MacNay, 1952), this insect has spread throughout the United States, except for several southwestern States (Anon., 1971), and throughout the cattle raising areas of Canada (Teskey, 1960). It has been called
one of the most serious livestock pests in these areas (Teskey, 1969).

The literature concerning face fly was first reviewed by Teskey (1960), and an annotated bibliography of face fly in North America has since been prepared annually (Smith et al., 1966; Smith and Linsdale, 1967, 1968, 1969).

One of the habits of the face fly which is of concern to farmers is the feeding habits of the females. They feed on mucoid secretions of cattle and horses, primarily around the eyes and nose (Ode and Matthysse, 1967). They may also feed on blood from wounds made by other insects such as tabanids (Hammer, 1941). The irritation and evasive actions of the cattle in response to these flies can cause a reduction of milk flow and reduced weight gain (Teskey, 1969).

In conjunction with their feeding, the face fly has been reported to transmit diseases and parasites. Human intestinal myiasis due to face fly was reported by Stephens in 1905 (cf. Teskey, 1960). Lamborn, in 1937 (cf. Teskey, 1960) believes that face fly may have been a primary vector of leprosy in Europe.

Several other diseases and parasites have been reported to be transmitted by the face fly. Among these are: conjunctivitis, infectious abortion, and the eyeworm Thelazia rhodesi (Teskey, 1960). Sabrosky believes that in California, the face fly may serve as a vector for the eyeworm Thelazia californiensis (see Teskey, 1960).

The second habit of the face fly which is annoying to man is its choice of hibernation sites. As the generic name indicates, Musca autumnalis has been called the autumn fly. This name refers to the fact that these flies hibernated in houses or other buildings beginning
in the fall. This has been well documented by Teskey (1960), who states that this aspect of the face flies' habits is the main topic of the literature on face fly from Great Britain. Teskey (1969) and Strickland, et al. (1970) report face flies hibernating in buildings and dwellings in Ontario, Canada, and California, respectively.

B. Life History, Habits and Ecology of House Fly and Face Fly

1. House fly. The life history, habits and ecology of the house fly have been studied by numerous authors. Reviews of these aspects of house fly biology have been published by Graham-Smith (1913), Hewitt (1914) and West (1951). The abundance of the literature regarding house fly biology causes a review of this literature to be a formidable task, and to become out of date quickly. West (1970) is compiling a bibliography of literature concerning house fly, which will be published shortly.

The house fly is a holometabolous insect whose larval stadia are dependent on environmental conditions, especially temperature (West, 1951). The stadia of the instars under normal conditions have been reported by several investigators. Their results are presented in Table I.

The geographical distribution of house fly has been said to be world wide. Graham-Smith (see West, 1951) qualified this statement to say that house fly is found everywhere that man is found, from subpolar to tropical regions. Within its geographical range, the house fly is found in and around dwellings, farms, and other places where fermenting crop wastes, garbage, or fecal matter is found (West, 1951). Around dairy farms, this insect may be found in the pasture, but is predominantly found in the barns.
The oviposition and feeding habits of the house fly have also been reviewed by West (1951). Preferred oviposition sites are fermenting substances such as garbage, crop wastage, and manure piles. House flies do not oviposit in cow pats found in the pasture (West, 1951), but prefer media which remain moist for several days, such as compost piles.

The adult diets consist mainly of carbohydrate and protein. Derbeneva-Ukhova was quoted by West (1951) as reporting that sugar or soluble starch is necessary for adult longevity, and that protein is necessary for egg maturation. This has been demonstrated more recently by Sacca and Benetti (1960), who showed that a diet of sugar and water did not inhibit spermatogenesis but did prevent oogenesis. The source of these nutrients may be any of the larval media, or secretions of wounds of animals.

House flies do not swarm for mating, rather the males wait for females to pass by them. The males wait on cows, windows, walls, etc. for females to pass within their range. When a female does pass within the range of the male, it darts out after the female and attempts to grasp her (Hammer, 1941); or if both are walking, the male makes a leap onto the female's back (Hewitt, 1914). The attempts at mating are not confined to conspecific females, any object of the appropriate size and color will be investigated by the male (Vogel, 1957). A more detailed description of the mating behavior of the house fly follows in a later section; however, the sites at which the sexes get together should be noted here.

Various aspects of the reproductive biology of house fly have been studied extensively. Gametogenesis has been studied by Adams and Hintz.
Adams et al. (1968), and French and Hoopingarner (1965). The generative organs of both sexes of house fly have been most recently described by Rivosecchi (1958). He also discussed copulation and the path of the sperm within the female.

The effect of male accessory gland material on the female has been shown to be a loss of receptivity on the part of the female (Adams et al., 1968; Riemann et al., 1967; Riemann and Thorson, 1969).

Other aspects of the reproductive biology of the house fly, such as the period of sexual maturation, time spent in copula, etc., have been studied by numerous investigators. Their results are presented in Table II.

Since house flies are diurnal insects, it would seem that light is a necessary factor in mating. Rogoff (1965) showed, however, that mating can take place in complete darkness, although no conclusions were drawn as to the relative importance of light in mating.

2. Face fly. The literature concerning the life history and habits of the face fly is far less voluminous than that concerning house fly. It has been reviewed by Teskey (1960, 1969).

Face fly is also a holometabolous insect whose stadia of the preimaginal instars are dependent upon temperature (Teskey, 1969). The length of the various stadia, as reported by several investigators, are presented in Table I.

The face fly is found in most of the Palearctic region of the world (Teskey, 1960). Within this geographical area, face fly is found associated with cattle and their excrement (Hammer, 1941), and also with horses (Teskey, 1969). The flies spend the daylight hours around
pasturing cattle (Hammer, 1941; Ode and Matthysse, 1967), and seldom enter buildings, except to hibernate (Ode and Matthysse, 1967).

The feeding habits of the face fly are the major source of its economic importance. Female face flies feed on mucoid secretions around the eyes and nose, blood from wounds, or manure. They have been called facultative blood feeders, for they can obtain the nutrients for oogenesis from either blood or manure (Teskey, 1960). The males feed primarily on nectar and are seldom found on cattle (Hammer, 1941).

Bovine feces, which are dropped in the field, are the primary sites for oviposition (Teskey, 1969). Teskey (1969) stated that attempts to rear face fly using pig, horse, and human feces were unsuccessful. All bovine feces are not satisfactory for oviposition; however, Teskey (1969) reported that the cow pats must be in the sun and that the manure must not be either too moist or too dry for the females to oviposit.

The sites at which the sexes meet for mating were described by Hammer (1941). According to his field observations, male face flies seldom go to oviposition sites to mate. If they are on the cow pat, they are there primarily to feed. He further states that face fly, and most other flies associated with cattle, meet on conspicuous objects in the field. Carts, a lone bush, or even a cow may serve as a meeting site. In the latter instance, the males are using the cow as a landmark, not as a food source. Hammer (1941) also stated that the male waits for the female to fly past and then darts out after her. After contact, the pair of flies tumble to the ground, presumably to mate. Teskey (1969) reported similar sites for the meeting of the sexes. In
addition, he reported that females walking on the same surface as males may be mounted by the males as they pass. The mating attempts of male face flies are not restricted to conspecific females. Teskey (1969) reported that male face flies dart out after flies other than their own species, and also at "... small bits of dirt thrown in front of them."

Various authors have studied different aspects of the reproductive biology of face fly. Valder (1969) described the morphology of the reproductive systems of both sexes. Oogenesis and gonadotropic cycles in face fly have been studied by Derbeneva-Ukhova (see Teskey, 1960) and Miller and Treece (1968), respectively.

Other aspects of the reproductive biology of the face fly, such as, the period of sexual maturation, time spent in copula, etc., have been reported by several authors. Their results are presented in Table III. The optimal age for mating was found to be 3-7 days of age (Teskey, 1969) and 5-6 days of age by Lohda et al. (1970).

The effect of light on mating was studied by Lohda et al. (1970), who found that face flies were able to mate in the dark, but that light increased the number of flies that mated. Teskey (1969) stated that mating does not occur in the dark, provided that the flies had a daily period of illumination.

C. Mating Behavior of Insects

The problem of reviewing the literature concerning courtship in insects is summed up by Engelmann (1970) who stated, "A vast entomological literature covers the various aspects of courtship in insects, and it is a formidable task to extract the essentials of today's
knowledge. Innumerable reports mention details of mating behavior and copula, but in relatively few cases is a full analysis available."

Despite the vastness of the literature on insect courtship, the muscoid Diptera have been almost completely neglected. Chapman (1969) and Manning (1966) further stated that there is no courtship behavior in the genus *Musca*. They believe that the male mounts the female and attempts to copulate with her without preliminaries.

To begin to fill the void in behavioral studies, one must draw upon principles, theories and terms used in the study of animal behavior. In this section, these terms and principles will be defined and explained, and general aspects of courtship will be reviewed. These aspects will include description of behavior in time and space, mechanisms, and function of courtship behavior, as well as the evolution and micro-evolution of courtship behavior.

These and other aspects of sexual behavior have been reviewed by Alexander (1964), Chapman (1969), Davey (1965), Engelmann (1970), Jacobson (1965), Manning (1966), and Richards (1927).

The type of behavior of interest in this study is directed towards another animal, therefore there must be communication between the animals. The mechanisms of communication will be discussed later.

For the purpose of this study, mating behavior or sexual behavior will be defined as, "... the events surrounding the insemination of the female by the male." (Chapman, 1969). This is a broad definition and includes such things as swarming, acoustical communication, epigamic recognition. Courtship is also an aspect of mating behavior and will be defined as, "... specialized behavior patterns which form the
normal preliminaries to mating" (Manning, 1966). The use of "courtship" will be confined to behavior patterns of males directed towards a potential mate, immediately prior to copulation or attempted copulation.

Description of behavior in time and space requires the segregation of a behavior sequence into clear-cut units. The units used in behavior are the fixed action pattern (FAP) proposed by Lorenz (1937). Fixed action patterns are stereotyped, species-specific movements which are independent of learning and are not influenced by environmental stimuli except for the one that elicits the behavior. Behaviorists regard FAP as the smallest unit of behavior. The FAP is a complex reaction to a single stimulus (a sign stimulus, or releaser). The entire courtship ritual of a species is not considered a FAP unless it is elicited by one stimulus. However, most courtships which have been analyzed have been comprised of a series of stimuli and FAPs (Chapman, 1969).

With this concept in mind, it is obvious that describing a sequence of behavior must be done arbitrarily at first. Experimental proof is needed before an empirical division of the sequence into FAPs can be made (Marler and Hamilton, 1966). Thus, the units used in this description are arbitrary FAPs which are grouped or separated by their observed relationships with each other. Marler and Hamilton (1966) reviewed the procedures and problems of describing behavior in time and space.

Functions of courtship. During a symposium of the Royal Entomological Society of London, Dr. Aubrey Manning reviewed sexual behavior in insects (Manning, 1966). A portion of this talk is the basis for the present review of the functions of courtship.
Richards (1927) presented a classic review of sexual behavior. In this review, he introduced a concept which he called "female coyness", that is, in some species, the females will not accept a mate readily. Instead, they require a certain amount of stimulation before they will mate. Stimulating the female, until she is ready to mate, is one function of courtship. This function has been demonstrated experimentally by Ewing (1964). He showed the importance of the wing area of male *Drosophila* on their ability to stimulate the female to mate. By cutting the wings of the males, he was able to demonstrate a straight line relationship between wing area and mating success.

Appeasement is the second proposed function of courtship. In its classical sense, appeasement applies to territorial animals. The female that intrudes into the male's territory must somehow signal her presence as a potential mate, and not as a rival. In another, more obvious sense, appeasement refers to the necessity of the male signaling his presence as a mate to a predaceous female. This type of appeasement is one function of the courtship of spiders. Male mantids also must appease the female; however, Roeder (1935) has shown that they have developed an anti-courtship, where the male tries not to signal his presence.

Regarding insects that are neither territorial nor predaceous, appeasement may be used in a much broader sense. Manning (1966) states that most insects avoid body contact with other insects. To overcome this normal avoidance of contact, the male must signal his purpose in the contact, or must divert the female's attention and/or block her escape route. Examples such as the gifts of male Empidids or the saliva
of male Panorpa divert the female's attention. Grasping the legs of the female as in Tipulidae (Stich, 1963) serves to block her escape. A male butterfly hovering in front of the female as she flies and deluging her with pheromone also serves as an example of this type of appeasement. In short, one function of courtship, appeasement, is to communicate to the female that she is being courted by a potential mate.

Synchrony of mating movements goes along with appeasement. Chaotic movements of each individual would decrease the chances of the two individuals assuming the correct posture for mating. Therefore, fine synchronization of the movements of the male and female is necessary for successful genital contact and copulation.

A third possible function of courtship which was enumerated by Manning (1966) is physiological maturation. In some insects (e.g. Schistocerca gregaria, cf. Manning, 1966) the presence of males cause rapid maturation of the ovaries of females. This function is not widespread, and as Manning (1966) states, due to the short adult life of many insects, "... ovarian development has to be complete at metamorphosis or await only some key dietary factor."

The fourth and final function of courtship is sexual isolation. The value of ethological isolation has already been discussed (cf. Mayr, 1963). Manning (1966), however, does not feel that the courtship behavior itself functions as an identifying agent. He feels, rather, that courtship functions to demonstrate and emphasize an identifying agent, whether it is a pheromone, wing color, or a sound. Thus, the behavior pattern of males may not be recognized by the females, but the elements of the pattern serve to emphasize the identifying
characteristics.

2. Mechanisms of courtship. Before discussing the mechanisms of courtship behavior, several basic concepts must be stated. The first concept is the widely accepted idea that much of insect behavior is based on stimulus-response reactions. That is to say, that insects respond directly to stimuli, external or internal, rather than thinking or planning behavior. FAPs are one type of stimulus-response reaction and form a major part of insect behavior (Ewing and Manning, 1967). Thus, stimulus-response behavior can be considered a type of communication between the source of the stimulus and the receiver.

In any situation where communication between animals is necessary, there are several possible mechanisms for communication: tactile, visual, auditory and chemical communication systems (Engelmann, 1970; Marler and Hamilton, 1966). It should be stressed at this point that whether the species involved is a cockroach (Barth, 1964) or Drosophila (Speith, 1952) complete analysis of the mechanisms of the courtship behavior have shown that more than one communication system is involved. For example, Barth (1964) has shown that chemical communication (pheromone) stimulates the male to court, while tactile stimulation by the female elicits copulatory thrusts. Since stimuli vary in degree (i.e. concentration of pheromones, size of objects, etc.), the name "optimal stimuli" has been given to stimuli which insure the proper response. However, overoptimal stimuli can be produced in the laboratory (Vogel, 1957; Magnus, 1958). These overoptimal stimuli elicit more or stronger responses than normal and will be of interest in a later section. Another point which should be mentioned is that visual,
olfactory, and auditory stimuli normally serve mainly to bring the sexes together and to initiate courtship, while contact chemoreception and tactile stimuli are important in courtship per se.

In this review the role of each communication system in courtship will be mentioned; however, specific examples will be reserved for the discussion. In addition, the degree of specificity of response will be mentioned as the result of receptor deficiencies or ambiguity of the stimulus. The role of the communication systems in Diptera will be discussed in a separate section.

The role of vision in the behavior of diurnal insects is, obviously, quite an important one. Engelmann (1970) states that the "Important visual stimuli for attraction of the sexes are movement, color and form, as can be demonstrated by experiments employing dummies." This is in agreement with the acuity or lack of acuity of insect vision. Insects can see contrast between light and dark, outlines or forms, motion, and some insects can see colors (Marler and Hamilton, 1966). However, details of an object are not seen by an insect (Marler and Hamilton, 1966). The lack of visual acuity can be termed a receptor deficiency, and may cause unspecific responses (Marler and Hamilton, 1966). In other words, insects may respond correctly to visual stimuli, or they may respond to an incorrect stimulus. For example, male butterflies of several species follow models of the appropriate shape and general color which are made to move in the female's characteristic flight pattern (cf. Engelmann, 1970; and Marler and Hamilton, 1966).

Dragonflies have, perhaps, the best form vision of any insect. They are able to discriminate size, movement and color as well as wing
transparency (Marler and Hamilton, 1966). All these characteristics help determine whether or not a male will approach another dragonfly. Although their visual acuity is quite good, they do approach females of other species (Moore, 1952), but leave and do not court them. Thus, the first phase of the courtship response, approach, is evoked by relatively unspecific visual stimuli. After the initial approach, further identification is made by more specific stimuli (Marler and Hamilton, 1966).

Over-optimal visual stimuli have been demonstrated in butterflies (Magnus, 1958) and in flies (Vogel, 1957). In both of these studies, the investigators reported that the males approached models, which were larger than the normal size range for the species, more readily than normal size models.

The role of the auditory stimuli in courtship behavior has received wide attention. According to Engelmann (1970), "This means of recognition becomes particularly effective in species which live low on the ground in grassland." Indeed, sound is utilized extensively in Orthoptera, although it is employed by some Homoptera and some Diptera. Reviews of this topic have been published by Engelmann (1970) and Alexander (1964).

Olfactory stimuli have received much attention, especially in cockroaches and moths, and will be mentioned only briefly here. Innumerable articles concerning sex pheromones and their specificity have been written. For a review of sex pheromones see Jacobson (1965). The view that pheromones are species specific and elicit specific responses from the proper male is widespread. In fact, Marler and Hamilton (1966)
state that male silkworm moths can detect only female sex pheromone. Some evidence has been brought forth, however, which disputes the specificity of pheromones and demonstrates that the pheromone of one species may act as an overoptimal stimulus for another species (Barth, 1937; Shorey et al., 1965).

Contact chemoreception and tactile stimuli are extremely difficult to separate from each other. Contact between known sensory areas (e.g. antennae or foretarsi) may involve transferring chemical stimuli or may involve tactile stimuli. Several cases of contact chemoreception have been established. In Orthoptera and Blattaria, the males have dorsal glands from which the females feed. When the female is feeding, she is in proper position to copulate, and is quiescent (cf. Engelmann, 1970). Engelmann also reports similar glands in several beetles. Also in cockroaches, antennal fencing has been shown to result in contact chemoreception (Barth, 1964).

Tactile stimulation has also been established as a mechanism of courtship in several species. In cockroaches, for example, Barth (1964) showed that as the female mounts the male to feed on the tergal gland, the abdominal tergites of the male are stimulated by female movement. In this case the analysis has been extensive. Florentine (1968) found abdominal vibration receptors in male roaches which do respond to female movements. Michelsen (1964) found that biting and tapping play an important role in mating behavior of some longhorn beetles.

As we have seen, all the modes of communication available to insects are employed in courtship. It should be stressed, again, that no one communication system is solely used in the courtship of any species which has been studied.
3. **Evolution of behavior patterns.** Evolution of behavior patterns is a widely studied topic. For reviews on the subject see Ewing and Manning (1967), Manning (1966) and Marler and Hamilton (1966). Several points concerning evolution of behavior are of interest to the present study.

The first point is the differentiation between evolution and microevolution of behavior patterns. Evolution of behavior deals with the origin of ritualized behavior. Microevolution deals with the changes in behavior patterns among closely related species. It is illogical to assume that an animal would have special motions for every signalling purpose (Manning, 1966). Therefore, the ritualized behavior such as FAP has been termed "derived activities" (Marler and Hamilton, 1966; Manning, 1966, 1967). Also, the activities in courtship patterns often have no relationship to their original function (Manning, 1966). The activities are ritualizations of normal maintainance activities such as feeding, preening, etc. In many cases, a "typical intensity" (Morris, 1957) has been evolved to make the signal unambiguous. In some cases, such as a male cockroach raising its wings to expose the tergal gland, the activities do serve a purpose. Many other activities also serve an immediate purpose. Wing movements of tephritids (Tauber and Tauber, 1967) and butterflies (cf. Manning, 1966) serve to display conspicuous marking, while the wing movements are derived from flight movements.

Microevolution of behavior patterns has been studied in many groups of arthropods. As in the case of evolution of behavior patterns, it is illogical to assume that related species would have extremely different behavior patterns. Ewing and Manning (1967), Manning (1966, 1967) and Marler and Hamilton (1966) stated that the primary changes in behavior
patterns between closely related species are changes in frequency of performance of a FAP and their form or emphasis. Thus, the behavior patterns of closely related species are truly homologous and the same FAP can be found in all the species.

An example of changes of frequency of performance of a pattern is given by Manning (1959). Two sibling species of *Drosophila* have similar courtship rituals, but one element in the ritual is used more frequently in one species than the other.

Difference in emphasis was exemplified by Crane's study (1957). He found almost identical courtship rituals in fiddler crabs. The main difference between species is the pattern of waving of the large colored claw. The genus can be divided into subgenera by morphological differences. Corresponding to this classification, one subgenus waves the claw vertically, while the other waves it laterally.

The identification of mutant genes in *Drosophila* has opened up new possibilities in the study of microevolution. In fact, Manning (1967) reviewed the behavioral differences between mutant strains of *D. melanogaster*. The mutations, bar eye, forked and hairy bristles, vestigial and dumpy wings, and yellow and black body colors, all have corresponding behavioral differences from the wild type.

To summarize, one can expect to see elements in courtship ritual which are derived from daily activities, and when comparing the ritual of two related species one can expect to find many of the same fixed action patterns.

D. Courtship in Insects

1. Other than Diptera. Due to the number of descriptions of courtship
in insects which have been published, little purpose would be served in reviewing them. Those descriptions, other than Diptera which are essential to the present study, will be presented in the discussion.

2. **Diptera.** Mating behavior in the order Diptera has not been studied extensively, except within the genus *Drosophila*. This review will present reports of mating behavior and courtship of several species in eight families of Diptera. The order in which the descriptions are presented follows the systematic classification of the families of Diptera given by Borror and Delong (1964).

With the species arranged in order of evolution, the elements of the courtship patterns may also be compared. The description of the patterns will be presented when they are available, for many of them show elements which are similar.

In the lower Diptera, swarming is a common method by which the sexes meet. Chapman (1969) reviews aspects of this phenomenon. The aspect of mating behavior of interest to this study is the interaction between pairs of flies. This interaction, or courtship, was described for a species within the family Tipulidae by Stich (1963). He reported on the courtship pattern of *Tipula oleracea*. His results indicated that tactile stimulation is the important communication system in this courtship. However, no results negating the possibility of contact chemoreception are available. The analysis of the courtship pattern disclosed a series of stimulus-response reactions. The pattern was rigidly fixed, while each element was somewhat flexible.

The normal courtship pattern of *T. oleracea* was reported to be as follows. Courtship is initiated when the male touches the leg of the
female. The male grabs the leg with his leg, at which point the female raises one or more of her legs, he then mounts the female and pins down her legs. The male licks the female's thorax and moves forward until he licks her head, then slides back along the female's body and makes genital contact. The female's role in courtship is two-fold. First the female raises her legs, then, if receptive, she remains passive and lets the male court and mate.

The mating behavior of Culicidae has been studied by many authors (cf. Clements, 1963). Roth (1948) reported on the sexual behavior of Aedes aegypti. In this report he describes the auditory stimuli which bring sexes together, and describes the courtship ritual. His observations on the meeting of the two sexes in a laboratory cage indicated that males tend to ignore females that are at rest. Males court only flying females, and pairs that are flying in copula or courting attract other males. Roth (1948) further described the mechanism of attraction of the male to the female. His study discounted olfactory attractants, and did not mention visual attraction, but rather pinpointed wing beat frequency of the female as the attractive force.

The legs of the male and female play a role in courtship of A. aegypti. Roth's (1948) description of the courtship shows that the male always initiates courtship by grasping the female's leg, usually the hind leg. The male and female are "belly to belly" during courtship. The male grasps the female with his fore legs, while the middle legs act to push the female's hind legs upward, or to move her abdomen into position for copulating. Once genital contact is made, the male's middle legs are placed on the tibia or the base of the tarsi of the
female's hind legs to keep them raised. At this point, Roth points out that an unreceptive female uses her hind legs to dislodge the male. Once copulation is established, the male's hind legs drop down from the abdomen of the female and hang suspended.

Courtship behavior in the Empididae has evolved along an interesting line. As their common name, balloon flies, implies, males of many species of the family offer "balloons" to the females during courtship. The evolution of "balloon-making," from offering bare prey to making empty "balloons," is reviewed by Engelmann (1970). Although the courtship pattern of these flies is not directly comparable to that of other families of the order, two factors are important. The first factor is the hypothesis offered by Engelmann (1970), which states that the "balloon" may serve to enlarge the outline of the fly, creating an overoptimal visual stimulus. Secondly, the prey or "balloon," serves to divert the female's attention, thus serving the function of appeasement (Engelmann, 1970).

Courtships in the acalypterate Diptera have been studied in the families Tephritidae and Drosophilidae. Tauber and Toschi (1965) and Tauber and Tauber (1967) have described the courtship of several Tephritids. In *Eulea fratria* (Tauber and Toschi, 1965), the parsnip leaf miner, courtship begins with both sexes holding their wings at right angles to the body, with the costal margin dorsal. The wings are then waved alternately. During these displays of what the authors consider visual cues, the insects approach each other in a sidestep. No description of mounting is given, but once mounted and in genital contact, the male is said to have forelegs on the female's abdomen and hind legs
hanging. If the female's abdomen is depressed against the substrate (in rejection), the male uses its middle and hind legs to move the abdomen into position. Female rejection movements include not parting wings, keeping the abdomen down on the substrate, and kicking with the middle and hind legs.

The courtship of the gall-former Aciurina ferruginea, was described by Tauber and Tauber (1967). According to their description, both sexes of this species raise one wing at a time. One wing is brought out to a right angle with the body and twisted with the costal margin dorsal, then returned and the sequence is repeated with the other wing. The authors believe that as in E. fratria, visual stimuli are involved. They also mention the role of these visual cues in reproductive isolation. Mounting is accomplished by the male moving his head under the female's wing and moving so as to face in the same direction as the female and separating its wing at the same time. As the male mounts, his fore and midlegs keep the female's wings apart. While mounting, the male keeps his mouthparts in contact with the female's abdomen. In the copulatory position, the male's fore and midlegs are on the female's abdomen, with his hindlegs hanging down. Female rejection responses in this species are described as being the same as in E. fratria.

Although Diptera, in general, have been relatively neglected as far as mating behavior is concerned, Drosophilidae, especially the genus Drosophila has been studied extensively. Voluminous literature is available on descriptive, analytical, genetic and evolutionary aspects of courtship in Drosophila. Speith (1952) presented a monograph on courtship in Drosophila and described courtship in over one hundred
species. Obviously, the descriptions cannot be reviewed here. In addition, Brown (1964a, 1964b), Bastock and Manning (1955), Manning (1959) and others have since described and analyzed courtship of different species and mutant strains of *Drosophila*.

As in the case of the tephritids, drosophilids court the female before they mount. Several elements are common to most drosophilid courtship repertoires (Speith, 1952). Among these elements are tapping, some type of wing vibration, licking and mounting. Tapping initiates all *Drosophila* courtship (Speith, 1952). The male taps the female with his foretarsi and, according to Speith, this serves to identify the female as being of correct species. The male then performs a wing movement ritual which is species specific, and in many cases licks the female genitalia. Where licking occurs, Speith reports that the female assumes an acceptance posture, with wings spread and genitalia exposed. Brown (1964a) reports that in *D. subobscura* no licking occurs, and that the male separates the female's wings with his fore and midlegs while mounting. Repelling actions of female *Drosophila* include kicking with mid and hindlegs, hitting out with front legs, moving abdomen away, and wing fluttering (Bastock and Manning, 1955). Aside from repelling actions, the female's role is passive and the male's behavior is not influenced by the activity of the female (Brown, 1964b).

More detailed comparisons of the courtship and analysis of the courtship of *Drosophila* will be presented in the discussion.

Courtship in Chloropidae has been studied by Adams and Mulla (1968). They described the courtship of *Hippelates collusor* as being composed
of the male circling the female several times and approaching the female and touching her thorax with his mesotarsi. This sequence was reported to be repeated for as long as one hour. After completing this sequence, the male is said to jump on the female and initiate copulatory movements.

Parker has studied various aspects of the reproductive behavior of the Anthomyiid, *Scatophaga stercoraria*. Included in this study are male searching behavior, intersexes, epigamic recognition, and competition between males for females (cf. Parker, 1970a, 1970b).

Descriptions of mating behavior in Muscidae are extremely rare. In fact, only one description of the courtship of a muscid fly, other than face fly or house fly, could be found. Reports on mating habits (e.g., time to maturity, the number of times each sex mates) of Muscids are not as rare; however, they are usually included in articles dealing with the economic importance of the insect (cf. Harris et al., 1966).

The sole description of courtship in Muscidae, other than face fly and house fly, deal with two species of *Fannia*, *F. femoralis* and *F. canicularis* (Tauber, 1968). The initial approach in *F. femoralis* is made by the male towards a moving female (walking or flying). This indicates that movement and vision are important (Tauber, 1968). The situation is slightly different in *F. canicularis*, in that the males most readily approach flying females. Tauber stated that sound of wing beat may play a role in attraction.

The courtship of *F. femoralis* begins with the mounting of the female by the male. Tauber describes the activities of the legs during the precopulatory behavior. He stated that the male's foretarsi remain in almost constant contact with the female's thorax and wing base, while
the middle and hindlegs force the wings apart. The midlegs grasp the wings and hold them separated while the male slides back to make genital contact. After the hindlegs have spread the wings, they are said to "fence" with the female's hindlegs and midlegs. According to Tauber (1968), non-receptive females kick at the male, arch their abdomen to the substrate, do not spread their wings, and do not vibrate their wings. No description of the courtship of *F. canicularis* was given. The author did, however, mention homosexual activities in both species.

The literature concerning mating behavior and courtship of the other Muscids, house fly and face fly, will be dealt with in a separate section.

The mating behavior of several species of Calliphoridae have been studied. Bartell et al. (1969) studied sexual activities of *Lucilia cuprina*, and Parker (1968) studied the sexual behavior of *Protophormia terrae-novae*.

The males of *L. cuprina* are said to approach a prospective mate by walking, though they may fly directly onto another fly. Bartell et al. (1969) reported that the male approaches another fly, orientates toward it, and touches it with his foretarsi. The male may then leave or mount the other fly. Once mounted, the male orientates his body axis to lie parallel to the other fly, and moves backwards to make genital contact. A sexually stimulated male is said to move his body up and down, vibrate his wings or take a brief flight. The repelling actions of the female were given as kicking with mesolegs, kicking a mounted male with hindlegs and curling the abdomen down and extending the
ovipositor until it reaches the thorax. A persistant male was said to be dislodged by a frenzied burst of activity. Bartell et al. (1969) also reported courtship in all-male colonies. Finally, Bartell et al. (1969) also demonstrated the role of a pheromone in L. cuprina. They stated that olfaction of the pheromone stimulated the males, but that contact chemoreception of pheromones increased the stimulation.

Parker (1968) found no evidence of volatile pheromone in Protaphormia terrae-novae. Females and males are equally attractive to males. However, evidence was presented for a contact pheromone which elicits the continuation of the courtship by the male. The female is said to passively accept courtship, or actively repel the male. Courtship is described as beginning with a run to the female, the male then mounts the female and orientates so as to be facing the same direction as the female. The male then moves back and separates the female's wings with his abdomen and attempts to make genital contact. Homosexual activities are described and are said to be very brief. The male's reaction of prolonged courtship attempts is described as being similar to preening the abdomen with his hindlegs. The female rejection is said to be a well developed form of wing vibration.

Thomas (1950) studied the mating behavior of some Sarcophagidae. This report consists of field observations on the mating habits of several species of Sarcophaga. He reported that the flies mate on the food source, and that males court other flies regardless of sex and species. In fact, he stated that pseudocopula between members of different species and same sex is common. He believes that recognition of conspecific females is by trial and error, and that identification is
made after courtship begins.

E. Mating Behavior of House Fly and Face Fly

1. House fly. Observations of the meeting of the sexes of house fly in the field have already been discussed (see p. 18). Investigators studying the mechanisms of attraction of male to female house fly have found two communication systems in operation. Vogel (1957) found vision to be important, and Rogoff et al. (1964) and Murvosh et al. (1965) found a sex pheromone to be the close range attractant.

Vogel (1957) analysed the visual stimuli that elicit approach and mounting behaviors in male house fly. He stated that optical stimuli, other than those from conspecific females can elicit approach and mounting. Several characteristics of the models used affected their value as stimuli. Dark toned objects were said to be most effective, especially if they had spiked edges and a black center. Two dimensional models were approached readily, but only three dimensional objects were mounted. Size and proportion of length to width, within certain limits, affected the value of the dummy. Movement and visual flicker were also found to enhance the effectiveness of a model. Vogel also found that he could create models which were more attractive than female house flies.

The results of the investigations concerning the possible role of a female sex pheromone in attracting males indicated that a pheromone does attract males (Murvosh et al., 1965) and that this pheromone enhances mounting and courtship (Rogoff et al., 1964). The main point which was shown by the two studies was that virgin female house flies that were old enough to mate, were more attractive than virgin males, young females,
or mated females. More recently, Carlson et al. (1970) isolated a pheromone of the female house fly. They found that the pheromone \((Z)-9\text{-Tricosene}\) is only somewhat attractive to males, but that it stimulates the males to court. To further support the idea that olfaction is the mechanism of attraction in house fly, Rogoff (1965) showed that house flies are able to mate in the complete absence of UV, IR, and visible light. In addition, Cowan and Rogoff (1968) have shown that the degree of responsiveness of the male house fly to the female pheromone is hereditary. Ilse and Mulherkar (1954) stated, however, that optical, not olfactory, stimuli are the important stimuli in eliciting courtship.

Since there is good experimental evidence for both visual and olfactory stimuli being involved in attraction of male house flies to females, both of these systems should be regarded as having a role in bringing the sexes together.

The courtship of the house fly has been studied by different authors over centuries. Rogoff et al. (1964) cited Réaumur (1738) as saying that the courtship behavior of house fly was described in general terms by Aristotle. Berlese, in 1902, described the courtship of house fly. He stated that the male mounts the female, vibrates its wings, leans his body forward, leans back and tries to copulate. He further stated that the female controls whether copulation occurs or not, by either extruding her ovipositor or refusing to. Hewitt (1914) and West (1951) reported similar descriptions of house fly courtship behavior. Hewitt (1914) described the initial contact between male and female house fly as a strike. He defined a strike as ". . . a carefully calculated leap from a short distance." Thus in cases where both flies are walking, the male
leaps onto the female. In this study, the word strike will also be employed when referring to flies that are in flight.

Bishopp et al. (1915) mentioned that before copulation the male alights on the female, and that this action appears to be "... in the nature of courting." They mentioned female rejection as being composed of actions of the female's hindlegs.

Rivosecchi (1958) described and illustrated the courtship of house fly. According to his observations, a mounted male vibrates its wings so as to produce a low sound, and caresses the head of the female with its mouthparts. The illustrations show that the wings of the female are parallel to the substrate and at right angles to the body. The male then goes back and tries to copulate. A male that succeeds in grasping the female's ovipositor raises its abdomen and stretches the telescoped ovipositor, then returns to a position where the terminal abdominal segments are touching.

Murvosh et al. (1964a) presented a more detailed description of the courtship of house fly. Only the essentials of their description will be presented at this time. They stated that most males land on the female facing the correct direction; however, those males that land backwards or sideways right themselves quickly. When the male is facing the same direction as the female, the female's wings are said to extend to the horizontal flight position and vibrate rapidly, producing a buzzing sound. During this action, the male's hindlegs are said to lift the female's hindlegs to place them under her wings. The male then reaches forward and "caresses" the head of the female with its foretarsi. The male appears to "nuzzle" the female's head with his. The male backs
up and tries to make genital contact. At this point the authors state that the male's hindlegs are usually crossed under the female's abdomen, and the female's wings return to their normal resting position. Female rejection movements are said to consist of being passive and not extruding the ovipositor, or shaking the male off by violent struggling.

The above observations were made by the authors using a two power magnifying glass and, as they state, the actions were difficult to follow. The authors also mention homosexual behavior, and the presence of incomplete sex recognition on the part of the male house fly (cf. Murvosh et al., 1964).

Rogoff et al. (1964), while studying the role of pheromones in house fly mating behavior, described the courtship of the house fly. They mention the lack of sex recognition in the house fly and stated that males may strike females, males, or dead flies. Once mounted, the male is said to reach forward, stroke the head of the female with its foretarsi and settle back to make genital contact.

Cowan and Rogoff (1968) illustrated the courtship of house fly. According to their illustrations, the male mounts the female and leans forward and caresses the head of the female with its mouthparts. Simultaneously, the male is vibrating its wings and is said to be producing a buzz. The wings of the female are shown to be extended at right angles from the body with the costal margin dorsal. The hindlegs of the female are shown to be extended upwards pushing the abdomen of the male. The male is then shown to settle back to the mating position.

The final report of courtship in house fly is that by Soliman et al. (1968). They analyzed the courtship of house fly in terms of activities
similar to those seen in *Drosophila*. They described activities of the male while it was walking around the female. Their results indicated that the minimum courtship in house fly consisted of orientation and a jump. Their "jump" was described as the male mounting, leaning forward, caressing the head of the female with its foretarsi and settling back to copulate. In other words, their minimum courtship is what all other authors have termed courtship. The remaining elements of courtship which these authors present will not be dealt with here, for none of these activities were seen during the present study, or if seen, they were not involved with courtship. They reported the female rejection movements as kicking with any pair of legs or moving her wings.

Barber and Starnes (1949) and Patterson (1957) reported on the rejection movements of female house fly and their consequences. Both reports indicated that one means of rejecting courtship consists of fending off, or kicking. The results of kicking with either midlegs (Barber and Starnes, 1949) or hindlegs (Peterson, 1957), are a crippling of the male. The crippling was reported to be mainly wing damage. Both authors report that male wings are battered and frayed after a few days with gravid females.

The function of courtship in the house fly has never been studied. However, Ilse, in a question to Manning (Manning, 1966), stated that if appeasement in its broad sense is a function of courtship, then the house fly may have more of a courtship than has been indicated.

2. *Face fly*. Courtship and mating behavior of the face fly has been almost completely neglected. The reports of Hammer (1941) and Teskey (1960, 1969) on face fly mating in the field have already been mentioned.
(see p. ). The study of Killough and McClellan (1969) on the mating habits of the face fly has also been mentioned. None of these studies included courtship behavior.

The only description of courtship in face fly was reported by Lodha et al. (1970). They described a jump or strike similar to that of house fly. Their observations indicated strikes while walking, and while flying. Males were reported to strike females, males, and dead females. These authors stated that once the male has mounted, it grasps the female firmly and assumes the proper position for mating. During copulation, the male's forelegs were reported to be on the female's thorax, midlegs on the abdomen, and hindlegs crossed under the abdomen, a position similar to that of house fly. The authors also mentioned that copulating pairs of face flies were courted by other males. Finally, they mentioned that olfactory and tactile stimuli, as well as visual stimuli, play a role in attraction of the male to the female.

F. Hybridization

The bulk of the literature dealing with hybridization is concerned with improving plants or animals for agriculture or laboratory stock, with little work done on the barriers to hybridization. The literature concerning hybridization in insects can be divided into two main categories; reports on the success of experimental hybridization between two species or subspecies, and studies of the factors which prevent such hybridization. The first category contains reports on many groups of insects. Many reports have been concerned with mosquitoes. Burgess (1962) reported an *Anopheles gambiae* and *A. melas*, Dobrotworsky (1967)
on Culex pipiens complex, Horsfall and Brust (1962) on Psorophora sp.,

The only literature dealing with hybridization in muscoid flies falls into the first category. These studies were done on hybridization between subspecies or geographical strains of house flies. Patterson (1956), Sabrosky (1952), Sacca (1957, 1958) and Wagoner and Johnson (1968) reported various degrees of reproductive isolation between subspecies or strains of the house fly, but no attempts have been made to cross members of different species of the same genus.

The factors which prevent hybridization have been termed "isolating mechanisms" by Dobzhansky (cf. Mayr, 1963). The general types of isolating mechanisms have been categorized and reviewed by Mayr (1963). In this classification, geographic isolation has been excluded. Geographic isolation deals with populations which are separated by geographic features such as mountains, oceans, etc., and isolating mechanisms deal only with populations which are actually or potentially sympatric (Mayr, 1963).

Mayr's classification of isolating mechanisms includes two main categories: premating mechanisms and postmating mechanisms. In the first category, seasonal and habitat isolation, ethological isolation, and mechanical isolation act to prevent interspecific mating and wasting
of gametes. In the second category, gamete mortality, zygote mortality, hybrid inferiority, and hybrid sterility prevent the successful establishment of hybrid populations.

A brief explanation of each type of isolating mechanism is necessary. Seasonal isolation refers to the differences in breeding season of two or more species. Habitat isolation is due to the differences in habitat of the species involved. Ethological isolation has been called the most important class of isolating mechanisms in animals (Mayr, 1963), though Manning (1966) doubts the value of courtship behavior as an isolating mechanism. This class is composed of numerous, species-specific courtship patterns, which prevent random mating. Ethological isolation is of specific interest in the present study since interspecific mating attempts provide the investigator with another means of evaluating the importance of individual components of the courtship ritual of the species. The differences in the courtship patterns of related species has been widely studied in Drosophila sp. by Barker (1962), Brown (1964), Dobzhansky (1946), Ehrman (1964), Kessler (1962), and Speith (1952). These differences have also been studied in cockroaches by Barth (1964). Manning (1967) states that there are always small, but detectable differences in the mating behavior of closely related species. Mechanical isolation refers to the "lock and key" concept of insect genitalia, which was asserted by Dufour in 1844 (see Mayr, 1963). Although this concept does not hold true in all insects, some evidence has been found to support it, at least in some species (Mayr, 1963). Shorey et al. (1965) reported that in crosses between Heliothis zea males and H. virescens females, the insects succeeded in coupling, but no spermatophore was
transferred, and the insects were unable to separate.

Among the postmating mechanisms, gamete mortality and zygote mortality refer to the death of the sperm or eggs, and the death of the embryo, respectively. Patterson (1947) reported an "insemination reaction" in female Drosophila, in which the walls of the vagina swell and kill the sperm after interspecific matings. This type of reaction has not been reported in any other insect group. Another type of reaction in which the sperm from interspecific matings is immobilized was reported by Leahy and Craig (1967). They found that the sperm in the spermathecae of females from interspecific matings died soon after copulation. The mass in the spermathecae appeared to be, "gelled together in a viscous mass with no movement evident." (Leahy and Craig, 1967). Hybrid inferiority refers to the fact that although hybrids may appear to be fully fertile (they produce apparently normal eggs and sperm), they do not produce any offspring. Hybrid sterility refers to the well known phenomenon of varying degrees of fertility in populations of hybrids. For a complete review of these isolating mechanisms see Mayr (1963). Leahy and Craig (1967) provided a review of the barriers to hybridization between Aedes aegypti and A. albopictus.

A more detailed discussion of these isolating mechanisms and their role in preventing hybridization between house fly and face fly will be found in a later section. However, it must be made clear at this point that these isolating mechanisms seldom, if ever, act independently. They act together to achieve reproductive isolation. Also, they are not completely effective. See Mayr (1963) for a review of the breakdown of isolating mechanisms.
In a discussion of the methods for describing behavior in time and space, Marler and Hamilton (1966) reviewed the pitfalls and guidelines for describing and naming action patterns. The main points to emphasize are that descriptions should be objective, and that anthropomorphisms should be excluded. Names given to action patterns should be descriptive in nature, and should not imply a function, until the function has been demonstrated. Therefore, the term "caress", which has been used by several authors (cf. p. 42), will be discarded and replaced by the more descriptive term "lapping".

The following analysis is based on numerous observations of the courtship of house flies which were made using direct observation with a magnifier, and/or on eighteen courtship sequences which were recorded on 16mm movie film. All of the females that were filmed were immobilized as described previously. Observations of non-immobilized flies indicated that the same positions were assumed during courtship. Thus, there is no reason to believe that immobilizing the females has any adverse effects on the courtship behavior of either sex.

The action patterns described below are, at present, arbitrary divisions of a complex of action patterns. These divisions are not meant to imply any functions or neuro-muscular mechanisms of these patterns. Inferences regarding the functions of the patterns will be drawn in the discussion.

Many of these action patterns occur simultaneously, or overlap in
time. Thus, although the patterns are segregated for the purpose of describing them, they are not segregated in time. The primary criteria used in dividing the courtship into units were the appendages were involved and the order of occurrence of the units within the courtship sequence.

In many discussions of insect reproductive biology, sexual behavior, etc., the terms copulation, insemination, and coupling are used synonymously. Definitions of these terms are presented below to show the differences in their meaning as used in this study. The definitions are taken from Gwadz et al. (1971).

Coupling (pseudocopula): achieving the correct body position for copula, including genital contact, without the genitalia being in the proper connection.

Copulation (copula): assuming a position of body and genitalia which would allow insemination to occur.

Insemination (sperm transfer): the transfer of sperm from the male to the female. The sperm is retained in the reproductive system of the female.

Most females that were restrained for filming remained quiet prior to the strike of the male; however, they did move their appendages somewhat. The activity of females of both species that is of interest is extruding the ovipositor. Two female face flies and one female house fly were observed stretching their ovipositors to their full length and tapped the substrate. This action was similar to that seen when the females are ovipositing. This action had no apparent effect on the males present in the cage, and no function could be assigned to it.
A. Courtship of the House Fly

1. The normal male behavior. The stereotyped courtship behavior of male house flies is composed of a series of action patterns directed toward the female. Strictly speaking, the courtship begins when the male mounts the female, and ends when copulation is established. However, several elements immediately preceding mounting, as well as copulation itself, are included in the description of house fly courtship.

The normal action patterns of the male include: orientation, jump, landing, wing-out, leg-up, head lapping, head touching, boxing, backing, genital orientation, genital contact and copulation.

The normal elements of house fly courtship are being presented as representative of the courtship sequences that were uninterrupted and were performed with continuity between the elements. Those courtships in which the continuity of the elements was interrupted are considered under variations from the normal.

Within the normal sequences, allowances have been made for individual variation. Although individual variation is often used as a "catch all" for observed differences in the performance of experimental animals, there are valid reasons for such variations. Cowan and Rogoff (1968) reported hereditary differences in the responsiveness of the male house fly to the pheromone of the female. It is logical to postulate such differences in the behavior of the male that is elicited by this pheromone. Also, the insects used in this study were progeny of many different individuals of the stock culture. Finally, individual differences in the length of appendages would affect the exact position of
these appendages, and, indeed, of the entire body during certain elements.

**Orientation** (O), Fig. 1, A. Although orientation does not strictly fit into the definition of courtship, it is included as an element of the courtship pattern. For an animal to direct activities towards another animal or object, it must first orient towards it. Orientation may occur as an obvious body posture in some animals, and the male house flies were occasionally observed stopping and turning towards the female before the strike. More often, however, no such orientation posture was observed. Males resting on the side of the cage were observed flying out after females flying past. Males in flight were observed to strike other flies in flight or to land on resting flies. Male flies that were walking on the cage were observed to strike resting females without stopping or turning. On occasion, males were seen to approach a female and contact her before mounting; however, this was extremely rare.

**Landing** (L), Fig. 1, B. The landing of the male on the dorsum of the female is the first body contact in courtship. This action demonstrates one aspect of orientation. Most landings occurred with the male facing the same direction as the female. Occasionally, the male landed facing the side or posterior end of the female. In these cases, the male changed his direction, or turned. Turning will be discussed later. Preparatory to landing, the male positions his legs for contact with the female. The male's legs are held with the femora almost perpendicular to the body, and the tibiae and tarsi hanging down. Contact is made with the prothoracic legs touching the anterior portion of the notum of the female. The mesolegs contact the inner margin of the wings of the female, and, apparently, also the side of the abdomen. The hindlegs are
held J-shaped with the open section of the curve anterior. The hindlegs contact the side of the abdomen of the female.

At the point of landing, the male begins to vibrate its wings. The wings are kept in constant motion throughout courtship until the male moves back to make genital contact. It should be kept in mind, that in all the following action patterns of courtship, except genital orientation and genital contact, wing vibration is occurring along with all the actions of the legs and mouthparts that are described.

Also, the position of the male's legs, unless otherwise noted, are: forelegs on the anterior margin of the notum of the female, mesolegs are on or near the wing base of the female, and the hindlegs are J-shaped with the apical tip resting on or near the base of the female's hindleg.

Wing-out (W-0), Fig. 1, C. The wing-out element of courtship is the phase during which the wings of the female are extended to a position at right angles to her body. The costal margins of the wings are dorsal. This element appears to occur simultaneously with landing. From strictly observational data, it is difficult to state whether the female extends her wings, or whether the male pushes them out. However, in three courtship sequences there was a slight lag between landing and wing-out. In these sequences 1/10, 1/12 and 1/30 seconds elapsed between the two elements.

Once the wings of the female are extended to the wing-out position, they remain extended for the duration of the courtship. Normally the wings return to their normal position over the abdomen of the female only after copulation begins.
**Leg-up** (L-U), Fig. 1, C and D. The leg-up element of house fly courtship occurs at approximately the same time as wing-out. The metathoracic legs of the male move from the side of the abdomen until the pretarsus rests on the base of the hindleg of the female. At this point the female may kick back with her hindleg. Whether she does so or not, the male slides his hindleg along the femor of the female's hindleg until it reaches the femoro-tibial articulation. Once in this position the male appears to pull the female's hindleg upwards and forward until it is over her wings. In the leg-up position, the female's hindleg is draped over her wings with the tibia resting on the wing, and the tarsi pointed upward and anterior. The hindleg of the male then returns to the base of the hindleg of the female. This action is extremely rapid, and usually requires only 1/32 second, although some males require 1/8 to 1/6 second.

**Head lapping** (HL), Fig. 1, C, D, and E. The head lapping phase of courtship begins either while the female’s hindleg is rising or immediately afterward. During this phase, the male moves his body forward and the posterior end moves upward. When the head of the male is slightly anterior to the head of the female, the male's body is at approximately a 45° angle to the female. As the male moves forward his proboscis is extended and he laps the head of the female. The lapping begins at the back of the head of the female, and continues until the male is lapping the frons. The mouthparts of the male appear to be on the antennae of the female, or, at least, near them. The angle of the male’s head made the exact position of the mouthparts difficult to determine. The male continues lapping the head of the female throughout the next.
two courtship elements.

**Head touching (HT) and boxing (B), Fig. 1-E.** Head touching and boxing are two elements of house fly courtship that will be discussed together. They appear to be one continuous action, although different parts of the female are involved. As head touching begins, the female is in the wing-out, leg-up position, and the male is leaning forward at a 45 degree angle to the female and lapping her head. They remain in this position throughout the head touching and boxing phase. The male moves his forelegs from their position at the anterior margin of the female's notum or "shoulder" area. The foretarsi move along the head of the female and appear to rub over her antennae. At this point the female raises her forelegs and the male grabs them. This initiates the boxing phase. This phase is the longest phase of courtship, usually lasting 1/2 to 3/4 seconds. During the boxing phase, the male and female continually entangle their foretarsi. The motion of the foretarsi is circular.

**Backing (Ba).** When the bout of boxing has ended, the male is too far forward on the female to make genital contact. He must back up to bring his gentilia in close proximity to those of the female. The male replaces his forelegs on the notum of the female, slides his hindlegs along the side of the female's abdomen and assumes the position for mating. This position is subject to individual variation. At this point, the female is still in the wing-out, leg-up position. The forelegs of the male are either on the scutellum of the female, or near her wing bases. The mesolegs of the male are on the wing bases of the female, or on the proximal section of the wings. The hindlegs of the
male are placed under the abdomen of the female, and appear to raise the abdomen slightly. The tips of the hindlegs of the male remain on the base of the hindlegs of the female. The claspers of the male are extended while the male is backing. Once in this position, the male ceases to vibrate his wings. This position has been called the "male vertical pose" by Lamb (1922).

**Genital orientation (GO), Fig. 1-F.** Once the male has assumed the male vertical pose, he may not be in the proper position for genital contact, or the female may be unreceptive. In either case, if genital contact does not occur immediately, the male shifts his position slightly and keeps doing so for 1 to 2 seconds. During this phase, the male abdomen is continually moving towards and away from that of the female. Also, the claspers are continually trying to grasp the ovipositor.

**Genital contact (GC), Fig. 1-G.** When the male succeeds in grasping the ovipositor of the female, he raises his abdomen and stretches the ovipositor. Once the ovipositor has been stretched to its full length, the male lowers his abdomen and the flies remain with the tips of their abdomens touching throughout copulation. It is usually at this point that the female lowers her hindlegs and returns her wings to their normal position over her abdomen. This is possible because the male moves his hindlegs to a crossed position under the female's abdomen.

**Leaving (Le) and forward (F).** Leaving and forward are two phases of courtship which occur when the male is unable to effect genital contact. After 2 to 3 seconds of trying to establish genital contact, the male house fly may drop his hindlegs to the substrate and walk off the female, or drop his hindlegs and fly off. After leaving, the males
often return immediately and begin courting again.

Forward is a common element of house fly courtship. A male that is unsuccessful in establishing genital contact often moves forward and performs head lapping, head touching, and boxing again. The male moves forward by reversing the movements used in backing. The female is already in the wing-out, leg-up position.

Copulation (C), Fig. 1-H. With the establishment of genital contact, copulation begins. The position of copulation has been called the superimposed position (Hardy, 1944). The position of the male's appendages remain essentially the same as during genital orientation. The female is now free to walk, fly, feed, etc. The copulating flies are normally quiescent during copulation; however, if disturbed they do move. The female may fly short distances carrying the male. At the end of copulation, the flies become active, and part. Males have been seen to strike and court the female again.

2. Sequence and timing. The sequence and timing of the elements of house fly courtship appear to be subject to some variations. The variations are due to the ease with which certain movements (e.g. wing-out and leg-up) are accomplished. In many sequences, the hindleg of the female is down in one frame of film, and in the leg-up position in the next. That is, the leg-up action pattern lasted about 1/64 second. In other sequences, the action pattern could be followed through 6 to 8 frames (.1 to 1.8 seconds). This difficulty in performing one action pattern naturally causes the patterns to overlap.

The courtship, from landing until backing, lasts from slightly over 1/2 to 7/8 second. During 7/16 to 12/16 second of this time, the
insects are boxing. Backing requires approximately 1/12 second, and genital orientation from 1-1/4 to 3 seconds. Genital contact was not filmed; however, timing with a stopwatch indicated that it lasts only 1-1/2 seconds (see Table IV).

Assuming no difficulty in performance of any element of courtship, the sequence of action patterns in house fly courtship is as follows: The male orients and lands on the female, usually facing the same direction. As the male moves forward along the body of the female, he pushes her wings out and lifts her hind legs over her wings, as he begins lapping the back of her head. As the male moves further forward he brushes against the antennal area of the female's head with his forelegs, laps this same area, and reaches around the female's head and grasps her foretarsi with his. They remain in the boxing phase for a given amount of time, with the male at a 45° angle to the female. The male then slides back along the body of the female and positions himself to make genital contact.

3. Variations from the normal. The observations of normal courtship yields much information as to possible functions of the elements of courtship and their importance in the courtship ritual. However, variations from normal behavior and their consequences also yield much information.

Turning (T). Occasionally, the male house fly lands facing an improper direction. That is, he may land facing the side or posterior end of the female. Immediately upon landing, the male turns to face in the proper direction. There is no stereotyped pattern to this behavior; however, the males do continue to vibrate their wings while turning. An
interesting aspect to the male's landing in the incorrect position is that even though the male is in an improper position, the female's wings are moved out at right angles from the body, with the costal margin dorsal. This point will be discussed further in a later section.

**Inability to perform wing-out.** In several courtship sequences, the male was unable to perform the wing-out element of courtship. The female in all of these sequences was the same, therefore, it is assumed that either this female was able to prevent the element, or the pin which immobilized her interfered with the movement of the wings. Whatever the cause, the consequence of the fact that the males were unable to push the wings out is of interest.

One male that was unable to perform the wing-out, leg-up elements progressed briefly to lapping the back of the head of the female. However, he backed up slightly, almost immediately, and again vainly attempted to push the wings of the female with his mesolegs. The male then flew away. This entire sequence lasted less than 1/2 second.

A second male also attempted to push the female's wings out. He, however, did not progress to head lapping. Instead, he remained with his mesolegs on the inner margin of the female's wings for 1-1/4 seconds, then left the female.

The third male that was unable to perform the wing-out element also did not progress to head lapping. He remained on the female for less than 1/2 second, then left.

It is interesting to note that when the males were unable to push the wings of the female to the wing-out position, they were also unable to perform the leg-up element of courtship.
Inability to perform leg-up. In one courtship sequence the male was unable to lift the hindlegs of the female. This male spent slightly over 1/2 second in the head lapping, head touching and boxing phases, then spent 3/4 second in genital orientation before leaving.

Failure of the female to maintain wing-out and leg-up position. In one sequence, the male spent 5/6 second performing the normal courtship elements prior to backing. While the male was performing genital orientation the female was able to lower her hindlegs and return her wings to their normal position over the abdomen, 1/6 second later, the male departed.

4. Role of the female in courtship. The active role of the female house fly in courtship, if it exists at all, is very minor. Although no experimental evidence has been found, observations indicate that the male does perform the wing-out and leg-up elements. The only activity of the female during the courtship elements before backing is her role in boxing. This role is not clear, however. The male may be controlling the movements of the forelegs of the female, or the female may be actively participating. During the genital orientation phase of courtship, the female normally attempts to lower her hindlegs from the leg-up position.

Although the female's role in courtship is minor, she appears to control establishing genital contact. Observations indicate that the male is unable to grasp the ovipositor unless the female first extrudes it slightly. Thus, the female may passively accept courtship, and then not extrude her ovipositor. She may accept courtship and allow genital contact and copulation or she may reject courtship completely.
5. Rejection activities of the female. The most obvious rejection, failure to allow genital contact, has already been mentioned. In addition, the female attempts to stop or avoid male courtship in several other ways:

1. The female may decamp and avoid the strike.
2. The female may kick up at the male with either her middle or hindlegs.
3. The female may struggle violently to shake the male off. In this case, both flies whirl around on the substrate for several seconds.
4. If the female is able to lower her legs from the leg-up position, she may kick the male, or rub her legs along the top of her abdomen as in preening.
5. The female may lower her abdomen to the substrate so the male cannot achieve the correct position for coupling.

B. Courtship of the Face Fly

The description of the courtship of face fly will be brief. Many of the elements of the face fly courtship are extremely similar to those of house fly, and several of them are missing. To expedite the comparisons that will be made later, the arrangement of the courtship elements used for house fly, will be employed here. The following descriptions are based on numerous observations made without photographic aids, and also on ten sequences recorded on movie film.

1. The normal male behavior. Orientation (0), Fig. 2-A: The orientation phase of face fly courtship is identical to that of house fly. No
distinct orientation posture was observed; rather, the males darted out after or leaped on females and began to court.

**Landing (L),** Fig. 2-B. The posture of the male immediately prior to landing is the same as that of the house fly. The initial contact, however, is different. Male face flies land with their forelegs on the thorax of the female, the mesolegs on the female's wing base, and the hindlegs on the wings of the female. Normally, the hindlegs of the male do not remain on the wings, but move to the inner margin of the wings, or on the side of the abdomen. At this point, the hindlegs may hang down to the substrate.

As in the case of the house fly, the male face fly begins to vibrate his wings on contact with the female, and continues to vibrate them throughout the courtship until he assumes the position for genital orientation.

**Leg-up (L-U),** Fig. 2-C and D. The leg-up element of house fly courtship is modified in face fly courtship. Male and female face flies touch hindlegs. This element appears to be in the nature of fencing.

**Head lapping (HL), head touching (HT), and boxing (B),** Fig. 2-C, D, and E. These three elements of courtship are all present in face fly courtship. There is, however, one major difference between house fly and face fly. House fly males assume a position with their bodies at a 45° angle to the female. Face fly males, on the other hand, assume a position almost parallel to the female. During these phases of courtship, the forelegs of the male are in contact with the head and forelegs of the female, the mesolegs are in the area of the wing base of the female, and the hindlegs remain hanging along the side of the female's abdomen.
Backing (Ba). Face fly males, upon completion of the boxing element, slide back along the body of the female, separating her wings with their abdomens. Their forelegs are placed on the scutellum of the female, the mesolegs are on her wings, grasping the costal margin with the tibia above and the tarsal segments folded below the wing. The hindlegs of the male are positioned below the female's abdomen and pull it upward from the substrate.

Genital orientation (GO), Fig. 2-F. This element is an extremely long phase of courtship in face fly. The male is in the position described above with his claspers exposed. The hindlegs of the male may hang down along the side of the female's abdomen and touch the substrate. The male spends 20-30 seconds readjusting his position, pulling the female's abdomen upward, and trying to grasp the female's ovipositor with his claspers.

Genital contact (GC), Fig. 2-G. Filmed sequences show that in face fly courtship, as in that of house fly, the female controls whether or not copulation occurs. The male is unable to grasp the ovipositor of the female unless she first extrudes it slightly. Once the ovipositor is extruded, the male grasps it and raises his abdomen to stretch the ovipositor to its full length. He then lowers his abdomen and the flies remain with their abdomens touching throughout copulation.

Leaving (Le) and forward (F). Face fly males that fail to copulate depart from the female in a manner similar to house flies. Forward is a rare element in the courtship of face flies. Only one male was observed moving forward on a female to repeat head lapping, head touching, and boxing.
Copulation (C), Fig. 2-H. Face flies copulate in the superimposed position. The position of the male's appendages during copulation are: forelegs on the scutellum of the female, mesolegs on the area of her wing base, and the hindlegs under her abdomen. The male's hindlegs were observed to be either crossed or not crossed under the female's abdomen. As in house fly, female face flies are free to move and feed during copulation.

2. Sequence and timing. The sequence and timing of the elements of face fly courtship are far less complex than that of house fly. The male lands on the female, leans forward and performs the head lapping, head touching, and boxing phases of courtship. The time from landing to head lapping is approximately 1/10 second. The other three elements prior to backing are performed simultaneously and last from 5/6 to 9/6 seconds. Genital orientation is performed for 20 to 30 seconds. Successful genital contact lasts 1-1/2 to 2 seconds (see Table IV). The time that face flies remain in copula is given in a later section.

3. Variations from the normal. As has been shown, variations from normal house fly courtship are mainly due to difficulties in the wing-out leg-up elements. These elements are not present in face fly courtship, and no interrupted sequences were observed.

The only variations that were seen in face fly courtship were turning and side orientation.

Turning. Several male face flies landed facing an incorrect direction. All of these males, except one, turned immediately to face the same direction as the female. The one male that did not turn performed the entire courtship ritual, through genital orientation, while facing
the posterior of the female.

Side orientation. Two male face flies performed the entire courtship ritual without variation, until they backed on the female. During backing, these males moved to a position on the side of the female, instead of the superimposed position.

4. Female responses. The responses of female face flies during courtship and in rejecting courtship are similar to those of female house flies. The obvious exceptions are those responses of female house flies to the wing-out and leg-up elements.

Several female face flies performed a unique response. They shook their head from side to side. Without anthropomorphizing or implying function, the movement was similar to the human head shaking that signifies a negative response. The function or significance of this action is unknown.

C. Interspecific Courtship

1. Male house fly and female face fly. Films and observations of the mating attempts of male house flies towards female face flies indicate that the duration of the strike and the courtship elements performed are variable. The strikes lasted from 1/2 to 7 seconds, and the elements present seemed to depend on the responses of the female.

The elements present. Upon landing on a female face fly, the male house fly attempts to perform the courtship ritual of his species with varying degrees of success. No male house fly was able to perform the W-O or L-U elements. One male did, however, move the wings of the female slightly forward, and raise her hindlegs to approximately 45° from the
substrate. Most males merely succeeded in positioning their hindlegs between the abdomen and wings of the female.

In all of the sequences filmed, the males performed HL, and HT. Two males were unable to proceed to B. They stroked the head of the female (eyes and frons) with their foretarsi, but no boxing followed. Both of these males ceased courting at this point.

Of all the males observed courting, only one was unable to assume the GO position. This male ceased courting at this point.

The position of the appendages of the males during courtship was similar to their position in intraspecific courtship. However, the position of the female’s wings caused some variation. The hindlegs of the male remained between the abdomen and wings of the female. During GO, the midlegs of the male were on the proximal end of the costal margin of the female’s wings. His hindlegs were placed under the tip of the female’s abdomen.

One successful copulation was filmed, and the GC and C elements were identical to those of both species.

Timing. The time spent performing the courtship elements from L to Ba was 3/6 to 5/6 seconds. Those males that assumed the GO position, remained in that phase for 2 to 6 seconds. GC required 1-1/2 to 2 sec. The males that were unable to elicit B courted for 1/2 sec., although one stopped courting and remained on the female for an additional second.

2. Male face fly and female house fly. No mating attempts were observed between male face flies and female house flies.
D. Homosexual Activities and Epigamic Recognition

At this point, it is necessary to mention homosexual activities and epigamic recognition in house fly and face fly. Homosexual activity may be defined as male sexual activity which is directed towards another male. Epigamic recognition may be defined as the ability of a male to recognize a conspecific female that is physiologically ready to mate. According to these definitions, male sexual activity towards another male should be considered under epigamic recognition since it demonstrates the inability of the males to recognize a suitable mate.

No formal experiments were done on these aspects of house fly and face fly mating behavior; however, several observations made during the course of experimentation are germane to this study. These observations will serve to elucidate some of the aspects of the courtship behavior of these species.

Homosexual activities, in both species, are normal occurrences, regardless of whether females are present or not. In cages of isolated virgin males of either species, male-male strikes are seen frequently. These strikes, however, normally end as soon as contact is made.

1. House fly. House fly males are, occasionally, extremely persistent in their homosexual strikes and attempt to perform their courtship ritual, leave, and return to the same male. In addition, homosexual activities of male house flies directed towards male face flies were observed when these flies were placed together. In this case, also, the striking males were extremely persistent in their courting attempts.

Homosexual activities were not confined to the laboratory flies.
Field observations revealed that male house flies dart out from their resting places after many flies other than female house flies. One observation of this activity involved three male house flies stationed on the doorpost of a dairy barn. One male mounted another, and the two flies flew out several feet, circled each other and returned to their original positions. This sequence was repeated among the three flies.

In addition to courting other flies, male house flies were observed to mount their own empty puparia, dead flies, and a small, dark beetle which was placed in the cage. Normally, these encounters ended on contact; however, two males were seen repeating their courtship ritual on the puparium two or three times before dismounting.

Although quantitative data are not available on the effect of the presence of a female on the homosexual activities of males, it was noted that the presence of a female with the previously isolated males seemed to increase the number of homosexual mating strikes. The presence of a courting or copulating pair of flies also increased the number of mating strikes—heterosexual as well as homosexual. Many of these strikes were directed towards the coupled pair.

2. **Face fly.** Face fly males were less persistent in their homosexual activities. The most persistent of these activities were observed in a holding cage of 16 day old virgin males. Many strikes and three pseudocopulations were seen in this cage. Most of the strikes were brief, but the three pseudocopulations lasted 4 minutes, 2 minutes, and 45 seconds.

Male face flies were also observed courting their own puparia. This is more unexpected than house flies courting their puparia, for the puparium of the face fly is white. One male was seen repeatedly courting
a puparium and extending his genitalia in attempts to copulate. This male remained on the pupal case for 13 minutes.

Homosexual activity among face flies was not observed in the field; however, no field observations of face fly sexual activity were made.

The effect of the presence of a female on homosexual activities of face fly is similar to that in house fly. When a female face fly was introduced into a cage of male face flies that were exhibiting homosexual activities, these actions increased while the female was ignored. A frenzy of mating strikes occurred when males attempted to court the female. They were directed at the courting pair and other males. Not only did the number of strikes increase, but the males were more persistent in their courting.

3. Interspecific homosexual activities of male house flies and male face flies. Homosexual activities were not restricted to strikes at conspecific males. Many mating strikes were seen in cages containing male house flies and male face flies. The interspecific strikes were made only by the house flies. Normally, the strikes lasted only 1/2 second; however, some males were persistent and completed the ritual. These males assumed the position of pseudocopula. Strikes by several male house flies at one male face fly were not uncommon.

The reactions of the male face flies to being courted were frenzies of activity in an attempt to dislodge the courting male.

4. Multiple male courtships. As has previously been mentioned, males of both species strike at copulating or coupled pairs. When one male is in the GO position (copulating or performing GO), another male may land, and perform HL, HT, and B on the female. The second male then backs
over the first male and assumes the GO position on him. This sequence
may be repeated by another male, and results in chains of 2 - 4 males.
Multiple male courtships were not confined to conspecific pairs. Male
house fly and female face fly pairs were courted by other male house
flies.

E. Comparison of the Courtship Ritual of House Fly
and Face Fly

Comparisons of the courtship rituals of these two species can best
be presented in tabular form (cf. Tables IV and V); however, some addi-
tional explanation is necessary.

Most of the elements of house fly courtship are present in that of
face fly. Wing-out, Leg-up and Forward are not present in the face fly
ritual. Leg-up is modified to a fencing of the hindlegs of the two flies.
Forward, which is common in the ritual of house fly, is very uncommon to
face fly.

Two other elements of face fly courtship differ slightly from the
same element in house fly. Male face flies land with their hindlegs on
the wings of the female. The legs of male house flies are between the
wings and abdomen of the female during landing.

The position of the male during B also differs in the two species.
House fly males assume a position at a 45° angle to the female, while
male face flies remain parallel to the female.

Timing. The time spent in the various phases of courtship are simi-
lar in the two species, with two exceptions (cf. Table IV). Male house
flies spend $7/16 - 12/16$ seconds in HL, HT, and B, while male face flies
spend $5/6 - 9/6$ seconds in these activities. Genital orientation is the second exception. Male house flies readjust their position on the female for $1-1/4 - 3$ seconds while attempting to make genital contact. Male face flies remain in the GO position for $20 - 30$ seconds. This difference corresponds to the fact that male house flies perform F frequently, while male face flies tend to remain readjusting their position.

F. Experimental Hybridization

The first experiment of this series was designed to determine if interspecific copulation and insemination would occur. Fourteen pairs of female face flies and male house flies were placed together in one cage (cage A) and an equal number of pairs of female house flies and male face flies were placed in another cage (cage B). The cages and experimental conditions were described previously. The flies were observed at hourly intervals between the hours of 9:00 a.m. and 10:00 p.m. for three days. Mating attempts, if any, and copulating pairs, if any, were noted.

During the course of the experiment, eight copulating pairs, and many attempts at copulation were observed in cage A. No copulation, and no attempted copulation was seen in cage B.

On the fourth day of the experiment, the flies from both cages were killed and examined for broken wings since this criterion was considered as an indicator of mating attempts by Barber and Starnes (1949) and Patterson (1957). The wing damage corresponded to the observations of copulation. The wings of the majority of flies, both sexes, in cage A had been broken to some extent. The degree of damage to the wings of
both sexes ranged from no damage or slight ripping of the apical tip of the wings to the complete loss of the wings. The amount of wing damage per fly was greater in the males. The wings of the flies in cage B were undamaged.

The female flies from cage A were dissected to determine whether the copulations had resulted in successful transfer of sperm. The spermathecae and lateral sacs of all the females were devoid of sperm.

The second experiment in this series was undertaken to reaffirm interspecific mating, and to determine if sperm transfer did take place. A cage with twenty pairs of female face flies and male house flies was prepared. Two copulating pairs were isolated. One female face fly was dissected immediately after separation, and sperm was found in the fully distended lateral sacs. The second female, dissected one hour after the completion of copulation, had sperm in the spermathecae while the lateral sacs were not distended and were empty.

The remainder of the flies were examined for wing breakage after four days, with the results being that all female face flies had wings broken and all male house flies had wings broken or completely missing. The females were then dissected to determine if sperm was being stored in the spermathecae. No sperm was found in any female. Instead, a gelled mass was present in the spermathecae.

Experiment number three of the series was designed to determine whether the females from interspecific crosses would lay eggs, and if these would be viable. The two crosses were set up as in the first experiment, and manure was placed in the cages and replaced after two days.
Eggs were obtained from both crosses. One dish of manure, inadvertently, was left open in the room for one hour, while the other dishes were covered immediately with cheese cloth. One week later the dish left in the open contained pupae, while the other dishes contained no larvae or pupae. The manure which contained the pupae was considered to be contaminated with eggs of flies present in the room.

Since no copulation or attempted copulation was observed with male face flies and female house flies it was decided to concentrate on the cross between female face flies and male house flies. A cage was set up with approximately fifty pairs of flies. Twelve successful copulations were observed during the following two days. Manure was placed in the cages for oviposition after six days and removed two days later.

The manure was examined for eggs. Twenty-two eggs were found. These were removed and examined for embryonic development. Fifteen eggs had no sign of embryonic development. Seven eggs had early embryos. A developing tracheal system was seen, and in one embryo, peristalsis was observed in the gut.

Once embryos were found, another cage with twenty-five pairs of female face flies and male house flies was set up and provided with manure twice a week for three weeks. The manure was examined for eggs. One half of the eggs found were examined for embryonic development, while the other half was covered and allowed to remain undisturbed for one week, after which time the manure was examined for larvae and/or pupae.

No embryos were found in any of the eggs examined. None of the eggs left undisturbed hatched; rather, they began to turn brown and decay.
After four weeks, the flies were removed and examined for wing breakage. As before, all the flies' wings were broken or missing. The females were dissected and the spermathecae examined for sperm. No sperm were found.

A final experiment in this series was undertaken to obtain hybrid larvae. Cages of five female face flies and ten male house flies (cage A) and eighteen female house flies and thirty-six male face flies (cage B) were set up as before. After one week, manure was placed in the cages everyday for three days. Eggs were obtained from both cages and set aside as before to hatch and develop.

During the course of the experiment, many copulations were seen in cage A and two copulations in cage B. This was the first time that any mating had been observed in the cage with male face flies and female house flies.

After five days, eighteen face fly pupae were found in the manure from cage B. No larvae or pupae were found in any of the other oviposition dishes. This, along with the observed copulations, caused some suspicion as to the types of flies in cage B. Examination of these flies revealed that one female face fly was present.

Further examination of the flies for wing breakage proved to be extremely interesting. All the male face flies had broken wings, the female face fly had no wings left and the female house flies had normal, unripped wings! No sperm were found in female house flies; however, the female face fly had sperm. The flies in cage A were examined, and all the flies' wings were broken. One female had sperm in the spermathecae (copulation was seen several hours before).
The situation in cage B prompted an additional experiment to determine if male face flies could, indeed, distinguish their own species, and if male house flies shared this ability.

The final experiment, termed a male choice experiment (Sacca, 1957) consisted of two combinations of flies in the same type of cage used in the other experiments. Two replicates were prepared for each of the following combinations of virgin flies. The first two cages (A¹ and A²) each contained five female face flies, one female house fly, and five male house flies. The second cages (B¹ and B²) each contained five female house flies, one female face fly, and five male face flies. Intraspecific matings were observed in the cages within the first two hours of the experiment. After ten days, the flies were frozen and examined for wing breakage. The results are shown in Table VI and VII.

The results of the hybridization experiments are summarized in Tables VIII and IX.

G. Relative Success of Male House Flies in Overcoming Ethological Isolation

After determining that the male house fly X female face fly cross could result in sperm transfer, an experiment was designed to determine the relative success of male house flies in overcoming the barrier of ethological isolation. This was achieved by measuring the time between the introduction of the males with the females and copulation. In addition, the time spent in copula was recorded to determine if interspecific matings lasted long enough for sperm transfer to be accomplished, as
compared to reports of the minimum time necessary for intraspecific insemination.

This experiment consisted of four combinations of flies: male house fly X female house fly, male face fly X female face fly, male house fly X female face fly, and male face fly X female house fly. Five pairs of five-day-old virgin flies of the desired sex and species were placed together in a holding cage. The time at which copula was established and ended was recorded for each copulating pair.

Four pairs of house flies were copulating within seven minutes, while the fifth pair did not copulate until 78 minutes after the experiment began. The mean time before copulation was 20.4 min, with a range of 5-78 minutes. Face fly, on the other hand, required a longer time before copulation. One pair was copulating after 14 minutes, while the other pairs required from 1 to almost 5 hours before they began to copulate. The mean time before copula was 129 minutes with a range of 14 - 290 minutes. The male house fly X female face fly cross was less successful than the intraspecific crosses. Only two of the males succeeded in copulating. The two copulations began after 140 and 298 minutes. The average of the two was 219 minutes. No copulation occurred in the male face fly X female house fly combination.

The average amount of time that the house flies remained in copula was 64.4 minutes with a range of 56-71 minutes. These values for face fly were 55 min, with a range of 35-74 minutes. The amount of time that the male house flies and female face flies spent in copula is based on the two matings in this experiment, and three other pairs of this combination that were of the same age. The mean time in copula was 37.5
minutes, with a range of 30-64 minutes.

The results of this experiment are summarized in Table X.
V. DISCUSSION

A. Comparison of the Description of House Fly Mating Behavior and Courtship with that of Previous Authors

1. The courtship ritual. The results of the observations and films on the courtship ritual of house fly is in, at least, partial agreement with all of the previous reports. Early reports, such as those of Berlese (1902), Hewitt (1914), and West (1951), were very general in their descriptions. The present study does, however, confirm the pattern that they described.

The report of Rivosecchi (1958) is somewhat more detailed than the earlier studies. The results of the present study confirm his findings, with one exception. Rivosecchi reported that a buzzing sound eminated from the male during courtship. The author heard such sounds only infrequently during the observations of courtship. The buzz was heard only during courtships in which the female was not immobilized. Thus this sound could result from the contact of the flies with the substrate during the struggling actions of courtship.

The most detailed description of house fly courtship prior to the present study was presented by Murvosh et al. (1964a). Generally, their description and the present description are in agreement. Several details do differ; however, Murvosh et al. report that after landing, the wings of the female extend to the horizontal flight position and vibrate rapidly. This vibration is said to produce a buzzing sound. They further state that the male places the hindlegs of the female under her wings to support them.
The present study shows that, although the wings of the female do extend to right angles from the body, they are held with the wing surface perpendicular to the substrate, with the costal margin dorsal. The films demonstrate that the female's wings do not vibrate, but remain stationary. As mentioned above, the buzzing sound was not heard frequently enough to include it in the courtship ritual. In addition, the films demonstrate that the hindlegs of the female are draped over her wings, not placed under them. Murvosh et al., as well as the other investigators of house fly courtship, do not mention the boxing phase of courtship.

Soliman et al. (1968) approached the description of house fly courtship from a different standpoint. They described house fly courtship in terms similar to those used for Drosophila sp.. In other words, their description involved activities of the male prior to mounting. Such activities were seen only infrequently during the present study. Strikes of males towards flying females eliminates most of what Soliman et al. term courtship. The strikes of males towards standing or ambulatory females observed during the present study are in disagreement with all but one of the courtship elements described by Soliman et al. The "Jump" of their description was reported to be the minimum courtship necessary for mating. Their "Jump" includes all of the elements described in this study. Therefore, our results are in partial agreement.

2. Rejection responses of the female. The rejection responses of the female to courting that were enumerated in this study are in agreement with those presented by earlier investigators. The role of the female in courtship differs slightly. Previous authors have stated that
the role of the female in courtship is strictly passive. Preliminary observations seemed to confirm these reports. Further analysis of the films indicated, however, that the female plays an active role in initiating the boxing element.

Berlese (1902) reported that the female appeared to control the success of the male in establishing copula by extruding the ovipositor. This observation was confirmed during the present study.

3. Epigamic recognition and homosexual activities. Epigamic recognition and homosexual activities in house fly have been discussed by numerous authors (cf. literature review). The present study confirms the incomplete epigamic recognition in house fly, and its resulting in homosexual activities. Thomas (1950) stated that Sarcophagid males tried to mate with many flies on the oviposition media, regardless of their sex or species. Similarly, house fly is precocious in its sexual activities, and strikes at any object of appropriate size and color. As with Sarcophagids (Thomas, 1950) and Drosophila (Speith, 1952), identification of the object of a strike occurs after contact.

B. Comparison of the Description of Face Fly Mating Behavior and Courtship with that of Previous Authors

The courtship behavior of face fly has been reported by Lohda et al. (1970). Their description is, however, general in nature. The present study confirms their observations on the courtship ritual and female rejection responses, and presents further details.

The other aspects of face fly mating behavior, such as epigamic recognition and homosexual activities, that were observed during this
study agree with previous reports by Hammer (1941), Lohda et al. (1970), and Teskey (1960, 1969). Since so little work has been done on these aspects of the biology of this species, there is no further basis for comparison.

C. Appearance and Habits of House Fly and Face Fly as They Relate to the Nature of their Courtship

Before beginning a discussion of the mating behavior of, or hybridization between, house fly and face fly, one point should be made clear. The populations of flies that are being discussed are those which are in proximity to livestock, especially dairy cattle. As has been mentioned (see p. ), the face flies remain mainly in the pasture, while the house flies remain in or near the barn. The habitats do overlap, however; and house flies have been collected in the pasture, and face flies have been seen near the barns.

The larval medium for these two species is the same (i.e., cow manure), and the mucoid secretions and blood of the cows is fed upon by both species. House flies, however, prefer pig or horse manure to cow manure.

The courtship of house fly and face fly is unusual when compared to most other descriptions of courtship of insects. The entire courtship ritual of these species is performed with the male mounted on the female. With the exceptions of several families of Diptera, the courtship of other insects include some non-body contact elements. For example: cockroaches (Barth, 1964) fence with their antennae, and the male performs a wing display before the female mounts; Drosophila spp. and tephritids
perform a dance around the female before mounting (Speith, 1952; Tauber and Tauber, 1967).

It is probably for this reason, and the speed of the courtship, that the assumption was made that muscids have no courtship (Chapman, 1969; Manning, 1966).

The courtship of house fly and face fly may be termed a post mounting courtship. The explanation for this type of courtship may be found by examining the appearance and habits of these flies.

House flies, face flies and some other dung flies have very similar appearance to the naked eye. Both sexes are essentially dull grey and black flies with no striking patterns or colors and no identifying large structure such as the bulb of a scorpionfly, or the mandibles of dobson-flies. They are extremely agile fliers, and take flight at the slightest provocation.

Discriminating between the species in the field is a formidable task even for an experienced human eye. Insect eyes, as we have mentioned, are far less capable of detail vision than those of humans. Therefore, the ability of a male fly to discriminate the species or sex of a passing fly is probably lacking. This discrimination must be made by other than visual means. The inability to recognize the species of a passing fly is not complete, however. Male house fly and face fly do not strike completely indiscriminately. As Vogel (1957) showed, there are certain characteristics of an object that elicit the strike. One of which is size. There is a maximum and minimum size of an object that will elicit the strike.

Male house fly and face fly, then, recognize a dark toned object of
the appropriate size and shape to be a prospective mate. This relatively unspecific response is due to a receptor deficiency. That is, the eyes of the flies are unable to discriminate detail. As was the case in dragonflies (cf. literature review), a more specific identification of the passing fly is made upon contact.

Along with the lack of specific visual cues, the studies on the sex pheromone of house fly have indicated that its effect is far less dramatic than the pheromones of moths.

Thus the visual and olfactory stimuli which a male house fly or face fly receives from a distance are unspecific. In the areas where both flies are found, interspecific and homosexual strikes should be and are common, as was demonstrated in the male choice experiments.

More specific identification of the fly that is the object of a strike must be made during the strike.

In addition, the effect of the presence of a female on homosexual activity of males of both species indicate that a pheromone is present. This indication is demonstrated by the increased number and increased persistance of male to male strikes when a female was present. The strikes were not directed only at the female, indicating that the pheromone is not an attractant, rather, it is an excitant. This is in agreement with the results of Murvosh et al. (1965); Rogoff et al. (1964); and Carlson et al. (1971).

D. The Function of Courtship in House Fly and Face Fly

Before discussing the functions of courtship in these two species, certain premises must be stated. Firstly, the female is receiving
stimuli from the male. Secondly, the male is receiving stimuli from the female.

Of those functions of courtship presented by Manning (1966), the one that is most probably served by the courtship of house fly and face fly is appeasement in its broad sense. It has been stated that the male must identify the object that he has contacted. Moreover, the female must recognize what has contacted her. This communication takes place during the courtship.

Observation alone is not sufficient evidence for stating function or mechanisms of action. However, if one consults the literature concerning the function and mechanisms of courtship in Diptera, some analogies may be drawn to propose functions for the actions in the courtships of interest to the present study.

Each courtship element will be presented along with its probable function. After all the elements have been discussed, an overall picture of the ritual and the functions of its component parts will be presented.

Orientation. The function of orientation has already been suggested. To react toward something, an animal must orient to it. The possible mechanisms of orientation are visual, olfactory, and auditory. The probability that visual stimuli are the most important stimuli in orientation is discussed under the male choice experiment. The results of this experiment and the results of other investigators (cf. Rogoff, 1964; Tauber, 1968; and Vogel, 1957) indicate that visual, rather than olfactory stimuli are crucial to orientation. Also, the fact that numerous strikes are directed towards courting or copulating pairs of
flies (which present a larger image) is comparable to the carrying of a balloon by male empidids (cf. Englemann, 1970), and indicates the importance of vision in orientation.

The role of auditory stimuli (i.e., wing beat frequency) has not been studied in house fly and face fly; however, males do strike at standing or ambulatory females. Roth (1948) used the fact that male Anopheles aegypti do not strike at females that are not flying to demonstrate the role of audition in sexual attraction. Using the same logic, the case in house fly and face fly indicates that auditory stimuli are not important for orientation.

No evidence of olfactory stimuli being involved in orientation was found. The role of a pheromone in house fly and face fly is discussed under homosexual activities and epigamic recognition.

One more point should be mentioned here. Since male house flies and face flies strike from a distance, and land on the female, one can infer that these flies are able to judge distance.

Landing. The function of landing is obvious, to contact a potential mate. The action of male house flies and face flies that begins during landing, that is, wing vibration, is somewhat unusual. Chapman (1969) states that initiation of wing movement in Diptera is caused by a loss of contact with the substrate by the tarsi. He further states that this movement is maintained by wind movement on the antennae. It would seem, then, that the male would cease beating his wings when he contacted a substrate and stopped forward motion (as when landing on a female). The continuation of wing beating indicates that this activity is serving a purpose in courtship.
Speith (1952) proposes three possible explanations for wing vibration in *Drosophila*:

1) The female sees the wing movement.

2) The wing movement disperses an odor to the female.

3) The wing beat produces an auditory stimulus.

These three proposed functions are said to stimulate the female to mate. The first explanation may be disregarded, for both house fly and face fly will mate in total darkness (cf. Rogoff, 1965; Teskey, 1969). The other two explanations are equally possible. No male pheromone has been demonstrated in either species, and no role of auditory stimuli in courtship has been demonstrated in either species.

Although wing vibration may not appear to be important at first glance, Ewing (1964) has demonstrated that in *Drosophila melanogaster* approximately 80% of the sexual stimulation that is provided during courtship is due to the vibration of the wings of the male.

Wing-out. Wing-out is performed only by male house fly. Its function appears to be appeasement in the sense that it prevents the female from escaping. The mechanism of wing-out is somewhat puzzling. As has been stated (see p. 53) it cannot be determined if the female assumes this position, or if the male pushes the wings out. Films of males that had difficulty with the wing-out position and films of the house fly x face fly cross show, however, that the male appears to push the wings of the female out with his hindlegs. During this action, the mesolegs of the male are on the wingbase of the female. According to Chapman (1969) the movements of wings of Diptera are controlled by indirect flight muscles; therefore, the male may be exerting enough
pressure on the thorax of the female to activate these muscles.

The puzzling aspect of the wing-out element is that male and female Tephritids (cf. Tauber and Tauber, 1967) assume the wing-out position with no aid from another fly. Therefore, this position of the wings can be achieved voluntarily.

Leg-up. The leg-up element of house fly courtship functions as an appeasing action. Its function appears to be twofold. Firstly, this action further incapacitates the wings of the female, preventing her escape. Secondly, it prevents one of the female's rejection movements. Roth (1948) reported that male *Aedes aegypti* raise the hindlegs of the female to a position over her wings. He also stated that females try to dislodge courting males with their hindlegs. This rejection response of the female has also been reported in *Fannia* sp. (Tauber, 1968), *Lucillia* sp. (Bartell et al., 1969), and *Protophormia* sp. (Parker, 1968). Female house flies also reject courtship in this manner, but once the hindlegs are in the leg-up position they are unable to kick at the male.

The modification of leg-up to fencing in face fly is similar to the fencing described in *Fannia* sp. by Tauber (1968). The fencing inhibits the effectiveness of the kicking of the female in rejection of courtship and, perhaps, diverts her attention from other movements of the male. However, another possible function of fencing, and possibly leg-up, is communication. Chapman (1969) states that the hindlegs of Diptera are equipped with proprioceptors. There is also other indirect evidence for the presence of proprioceptors and chemoreceptors on the hindlegs of Diptera. *Aedes aegypti* females dip their hindlegs into the water
prior to oviposition, and they keep their hindlegs above the substrate and in motion when at rest (Clements, 1963). Both of these activities indicate a sensory function of the hindlegs. Furthermore, female house flies and face flies tap the substrate with their hindlegs during oviposition. Finally, house flies and face flies spend much of their active time performing preening activities. One function of preening is to clean sensory receptors. Thus, much time is spent preening the antennae and foretarsi. In addition, preening of the hindlegs is performed often.

Evidence of the presence of chemoreceptors on the legs of Diptera is well documented (West, 1951), and although no direct evidence is available to demonstrate the presence of proprioreceptors on the hindlegs of house fly or face fly, the facts presented above do form a basis for postulating their presence. Therefore, it is possible that the function of both the leg-up and the fencing elements are communication, either tactile or chemical.

Head lapping. Lapping of the body of the female by the courting male is common in the courtship of Diptera (cf. Table XI). It has been described in Tipula sp., Tephritidae, and Drosophila sp. Speith (1952) states that lapping stimulates the female. The type of stimuli involved is questionable. Stich (1963) reported that tactile stimuli are involved. Speith (1952), however, stated that chemical stimuli may also have a role in the courtship of Drosophila; and Zdarek (1970) stated that contact chemoreception is important in the courtship of Pyrrhocoris apterus L.
During lapping, the male may also receive stimulation from the female. This stimulation may result from chemical transfer or touch. Evidence for this chemical type of stimulation comes from the work of Carlson et al. (1971), who found the house fly sex pheromone to be located on the cuticle of the female.

Since the area of the female body that is the target for lapping is the antennal area, it is probable that the stimuli being transferred to the female are chemical.

**Head touching.** This action also probably functions in transferring chemical or tactile stimuli. The male touches the head and antennal area of the female. The same argument presented for head lapping applies here since both the antennae and foretarsi are equipped with chemoreceptors and proprioceptors.

**Boxing.** The response of the female to head touching is raising her forelegs. This response was demonstrated by the interspecific crosses in which boxing did not occur. The male did not reach down and grasp them, rather, courtship ceased.

Tapping and touching activities involving the foretarsi are present in the courtships of many Diptera (cf. Table XI). The only analysis of the function of tapping with foretarsi in courtship is based on *Drosophila* sp. Speith (1952) goes into detail while discussing experiments which demonstrate that male *Drosophila* can identify their own species by tapping with their foretarsi, and some species can even distinguish between the sexes by tapping. Also, Speith states that the female receives stimuli from the tapping. These results are applicable to house fly and face fly, for, as in *Drosophila*, these species have chemo-
and mechanoreceptors on their foretarsi.

From the above discussion, one can conclude that the touching of foretarsi during boxing results in mutual stimulation of the male and female due to the transfer of chemical, and possibly, tactile stimuli.

**Backing.** The function of backing is, obviously, to bring the male and female into proper position for copulation. Multiple male strikes demonstrate that the striking male backs until he comes in contact with the abdomen of the first male. This indicates that the distance over which the male backs is not crucial. Rather, stimuli, probably chemical, are received by the male to communicate his position relative to the body of the subordinate insect.

This may, however, be only one function. Since the work of Florentine (1968) on Abdominal Vibration Receptors in cockroaches, the possibility of mechanoreceptors in the body of an insect poses another function of backing. The numerous hairs on the body of the flies and the possibility of A.V.R.-like receptors in the flies indicate that the positioning of the male on the female may serve to elicit extruding of the ovipositor, as the stimulation of the A.V.R.'s elicits copulatory thrusts in cockroaches.

**Extruding the ovipositor.** This action is the controlling activity of copulation. If the female does not extrude her ovipositor slightly, the male cannot grasp its distal end and assume genital contact.

**Genital contact.** The stretching of the ovipositor by the male must function to straighten the reproductive tract of the female. This insures a clear passageway for the sperm.
Copulation. The function of copulation is also obvious procreation. The path of the sperm and mechanisms of copulation are not germane to this study. For further information on the mechanisms of copulation in Diptera, see Rivosecchi (1958).

Turning. The fact that male house fly and face fly that land facing an incorrect position turn immediately, indicates that there is something about the female that identifies her head. Similar inferences were made by Zdarek (1970) about the bug, Pyrrhocoris apterus. The males must be able to recognize the anterior from posterior of the female. This, alone, is evidence of chemical communication. By contacting the posterior end of the female, the male does not receive the proper stimuli, and turn to where the stimuli are correct. This suggests a gradient of pheromone concentration on the cuticle of the female.

Forward. This element of house fly courtship and its absence in face fly courtship will be dealt with under the comparison of the courtship of house fly and face fly.

E. Female Rejection Responses

Several species of Diptera in the genus Drosophila and the family Tephritidae have evolved special actions to signal rejection. Among them are extruding, wing flicking, and curving the abdomen under the body (cf. Speith, 1952; Tauber and Toschi, 1965).

Females of the other Diptera studied reject courtship by kicking at the male, refusing to extrude the ovipositor, struggling violently, and lowering the abdomen to the substrate. These responses are present in house fly and face fly courtship. They do not appear to function as
signals; rather, they are direct attempts to dislodge the male or prevent his making genital contact.

F. Overall Sequence and Function of House Fly and Face Fly Courtship

The overall sequence and function of the courtship of house fly and face fly is: the male orients, jumps, lands on the female, and vibrates his wings to stimulate the female. He blocks her escape by draping her hindlegs over her outstretched wings (house fly) or by holding her wings and fencing with her hindlegs (face fly). Once the female is unable to escape, the male stimulates the female and receives further stimulation by lapping and touching her head. During these activities, he is identifying himself as a male of the same species, determining what he has contacted, and communicating his purpose, as well as the mutual stimulation. The female's response is raising of the forelegs whereupon the bout of boxing occurs. Boxing further stimulates and identifies the flies. The male then assumes the position for copulation. At this point, the female controls the success or failure of the courtship. The male house flies attempt to further stimulate the female by repeating some courtship elements, while male face flies remain in the genital orientation. Genital contact occurs and functions to insure a clear path for the sperm.

G. Stimulus-Response Reactions in House Fly and Face Fly Courtship

As was stated in the results, one can learn much about the nature of courtship from the variations from normal. Failure to perform certain elements caused a cessation of courtship. An analysis of this
phenomenon yields information as to the stimulus-response reactions involved in the courtship.

The relative lack of specificity of the strikes of male house fly and face fly indicates that, at best, epigamic recognition in these species is incomplete.

Observations of male house fly and face fly performing their entire courtship ritual on an inanimate object such as their own puparia, would seem to indicate that the entire courtship is one FAP, elicited by a visual stimulus. However, other activities of the males indicate that a stimulus-response chain is involved.

That apparent contradiction of these observations can be resolved if one employs the idea of thresholds and states (Bastock and Manning, 1955). A normal level of sexual excitation in male flies is exemplified by flies that have reached sexual maturity, and have been in contact with females. It is a well established fact that deprivation of a stimulus causes a lowering of the threshold of response to said stimulus. Therefore, mature male house flies and face flies that have been isolated from females would be expected to have a lower threshold for sexual excitation.

The males that were involved in the persistent courting of their own puparia were approximately two weeks old. These males, then had been deprived of females for approximately thirteen days (house flies). In this situation, one would expect a strong response to a mild stimulus. Thus, other males and puparia elicited a persistent courting.

The males used in the behavioral studies were 3-5 days old. Thus, they had been deprived of female stimulus for only 2-3 days (face flies).
or 1-4 days for house fly. One would expect their threshold to be some-
what subnormal, but far less so than the previously mentioned males.

The activities, or absence of activities, which effected their
courtship ritual will be discussed with reference to their being evid-
ence for stimulus-response reactions.

Turning is the first variation from normal behavior which indi-
cates a stimulus-response reaction. The fact that male house flies or
face flies that land in an improper position quickly turn to face the
same direction as the female indicates that the male receives stimuli
from the female that identify her anterior and posterior ends.

The male house flies that were unable to perform the W-0 element
on their own females did not complete courtship. One male progressed
briefly to HL; however, he ceased this activity and left the female.
The other two males did not progress to HL; they left the female after
they were unable to perform W-0. The single male house fly that was
able to perform W-0, but not L-U, did complete courtship and attained
the GO position.

In the interspecific crosses, the male house flies were unable to
perform either W-0 or L-U; however, most did complete their courtship.

These results must be analyzed with the fact in mind that male
house fly appear to be more greatly attracted to female face fly than
their own species, as was demonstrated in the male choice experiment.
Using these facts the results indicate that under normal conditions
W-0 supplies stimuli necessary for progressing to the other elements of
courtship. In the case of the interspecific crosses, the female face
fly appears to provide sufficient stimuli for continuing courtship
without the W-0 stimuli.

The fact that failure to perform L-U does not inhibit the courtship responses of the male house fly supports the contention that the L-U element functions to prevent the escape and rejection responses of the female.

Failure to elicit boxing, as was the case in two interspecific crosses, caused a cessation of courtship. Both male house flies that were unable to elicit raising of the foretarsi of the female stopped courting after the head touching phase. This indicates that HT elicits raising of the foretarsi by the female, and that boxing stimulates the male to back and perform GO.

One male house fly was unable to assume the GO position. The wings of the female face fly prevented proper positioning. This indicates that there are stimuli involved which communicate to the male that he is in the proper position for GC. Likewise, the repositioning of the male during GO indicates that he does receive certain stimuli that indicate whether his position is proper. Presumably, these stimuli involve the contact between the genitalia.

There were few variations from the normal in face fly courtship. However, since the sequence and elements of face fly courtship are similar to those of house fly courtship, one may assume that similar stimulus-response reactions are involved.

Figures 3 and 4 diagram the probable stimulus-response reaction in house fly and face fly courtship. Possible mechanisms are presented in parentheses along the arrows between elements.
The results presented above, when analyzed using the concept of varying states and thresholds of sexual excitation, indicate that during the elements of courtship the male passes through several states until he is ready to mate. Insufficient stimuli from the female prevent the male from reaching the next state. Thus, improper responses to a courtship element cause cessation of courting.

Following this argument further, the threshold of each fly for each state will vary according to the individual's previous experience. Therefore, some males will continue to court when a stimulus is received, while the same stimulus may not produce the threshold in another male.

H. The Relative Importance of Some of the Elements of House Fly and Face Fly Courtship Using Time and Occurrence in Other Diptera as Criteria

The amount of time spent performing the elements of courtship, when viewed with the presence of these elements in other Diptera, can elucidate their relative importance in courtship. The amount of time spent in the various phases of courtship are presented in Table IV. The presence of the elements of house fly and face fly courtship in other Diptera are presented in Table XI.

In house fly, Head Lapping, Head Touching, and Boxing which are performed almost simultaneously, last 7/16 - 12/16 seconds. In addition, Genital Orientation lasts 1-1/4 - 3 seconds and wing vibration is continuous throughout courtship, until Backing.

The male licking the female or touching her with his foretarsi is present in the courtships of all the Diptera that have been studied,
except Culicidae and some species of *Drosophila*. These actions appear in HL, HT, and B of house fly courtship, and are performed for a relatively long period of time. Thus, HL, HT, and B appear to be very important in stimulating the female to accept a mate. In addition, the presence of a pheromone on the cuticle of female house flies (cf. Carlson et al., 1971) indicates that the male is receiving stimulation from the female during these activities.

Genital Orientation is, obviously, present in all courtship; and since it is the longest element in house fly courtship, it would appear to be extremely important. Without the orientation of the genitalia, genital contact and sperm transfer could not occur.

Wing vibration has been reported in three families of Diptera other than Muscidae, and in one other species of Muscid (cf. Table XI). Since it occurs continuously during courtship, it must be important. Indeed, as we have mentioned, Ewing (1964) found wing vibration to be vital to the courtship of *Drosophila* sp.

The Landing, Wing-Out, and Leg-Up elements of house fly courtship are extremely brief. These elements are similar to elements present in the courtship of several other dipterans. Their role in stimulating the female is questionable, however, and they probably function primarily to prevent the escape of the female.

Since the elements of face fly courtship are similar to those of house fly, the same arguments and examples can be employed to demonstrate their importance in that species. Fencing with the hindlegs in face fly, replaces Leg-Up and, also, probably functions to prevent the escape of the female.
I. Comparison of the Courtship Ritual and Mating Behavior of House Fly and Face Fly and the Microevolution of these Behavior Patterns

The mating behavior and courtship rituals of house fly and face fly are extremely similar. Both species meet in a similar manner and perform similar rituals. There are, however, several differences in the behavior of these species.

The amount of sexual activity of male house fly and face fly is one difference. During the course of experimentation, it was noted that male house flies courted and mated with female house flies in less time than did male and female face flies. While filming, male house flies provided numerous and frequent courtship bouts within several minutes of their introduction into the cage. Male face flies, on the other hand, ignored the female for a great length of time (up to 2 hours), before any strikes were observed. Even when the mating strikes began, they were not frequent. The experiment demonstrating the relative success of male house flies in overcoming ethological isolation provides quantitative data to support these observations (cf. Table X). Whereas four of the five pair of house flies were copulating within seven minutes after their introduction into the cage, the first face fly copulation did not occur until fourteen minutes after the start of the experiment. The average time prior to copulation for the five pair of house flies was 20.4 minutes, while the face flies averaged 129 minutes before copulating.

Further evidence to demonstrate that male house flies are more
sexually aggressive, and have a lower threshold for courting, is derived from the persistence of house flies in homosexual strikes. The concept of levels of thresholds in house fly and face fly courtship is presented under the sections entitled Stimulus-Response Reaction in House Fly and Face Fly Courtship (see p. 93). It suffices to say that the fact that male house flies are persistent in courting male face flies demonstrates their lowered threshold for mating and their higher level of excitation. Similarly, the fact that house fly males strike readily at inanimate objects, while face fly males strike less often at similar objects, indicates that male house flies are more sexually aggressive and possibly less discriminating than male face flies.

Finally, casual observations of the rearing cages of house flies and face flies showed that, when the adults in the two cages are of the same age, there are many more mating strikes in the cage of house flies than in that of face flies.

The differences and similarities in the elements of the courtship and time spent in each are presented in Tables IV and V. These comparisons must be discussed in terms of the microevolution of behavior patterns.

As was stated by Ewing and Manning (1967) and Manning (1967), within closely related groups or animals, one expects the differences in courtship behavior to be one of degree. In other words, the patterns should be similar with the main differences in form or emphasis, and frequency of performance.

Manning (1959) reported that the courtship elements of two siblings species of *Drosophila*, *D. melanogaster* and *D. simulans* are almost
identical. The major difference between the two species is the proportion of two types of wing activity. The two types, vibration and scissoring, are present in both species; however, D. melanogaster performs vibration in a much greater proportion to scissoring. The reverse is true for D. simulans.

The differences in frequency of performance of the two elements, Boxing and Forward in house fly and face fly courtship provide similar results. Although Boxing (along with Head Lapping and Head Touching) always occurs in both species, these three simultaneously occurring elements are performed for consistently different amounts of time in each species (cf. Table IV). As the data reveals, face flies spend approximately twice as much time in Head Lapping, Head Touching and Boxing as do house flies.

Moving forward, after a period of Genital Orientation to repeat Head Lapping, Head Touching and Boxing is common in house fly. Although Forward was observed in face fly, it is extremely uncommon. As is indicated in Table IV, face fly remains in the Genital Orientation position for far longer than house fly, while house fly performs Forward more frequently than face fly.

All these differences in frequency of performance tie in together to give a good picture of the states of levels of sexual excitation of the two species.

The idea that Head Lapping, Head Touching and Boxing stimulate the male to higher states of excitation has already been discussed (see p. 95). Combining this information with the data presented above, one can make several inferences:
1. Male face fly requires more stimulation to reach a higher state of sexual excitation, thus more time is spent in Head Lapping, Head Touching and Boxing.

2. Once the higher level is achieved, the male remains at this level for a long period of time; thus, male face fly spends a longer period in Genital Orientation.

3. House fly requires less stimulation to reach the higher states of sexual excitation. These levels are probably not maintained; thus, house fly spends less time Head Lapping, Head Touching and Boxing, but must repeat these sequences often to maintain the state necessary for Genital Orientation. Consequently, they perform forward more often.

A change in form of the elements of courtship between house fly and face fly is also present. The differences in the activities of the hindlegs of the courting pairs of each species is such a change. It has been proposed that the primary function of these activities is to prevent the escape of the female and also to prevent her kicking in rejection of courtship.

The fencing of the hindlegs of face fly and the Leg-Up element of house fly courtship appear to be, then, analogous actions. The fencing activities occupy the hindlegs of the female face fly, while the Leg-Up immobilizes the legs. This situation is similar to the claw waving in fiddler crabs (cf. Crane, 1957).

From this discussion, we find that the microevolution of the courtship of face fly and house fly agrees with the concepts of microevolution in that the same or similar action patterns are present with the primary differences being in form, emphasis, and frequency of performance.
J. Derivation of Some Courtship Activities

The concept of derived activities (Tinbergen, 1952) and typical intensity (Morris, 1957) have been mentioned previously (see p. ). A study of the derivation, ritualization and typical intensity of the courtship of house fly and face fly is beyond the scope of the present study. However, the proposed derivations of several of the courtship elements will be presented below. The derivation of most of the elements remains unknown. In the Wing-Out element of house fly courtship the wings of the female are in a position that resembles one of the positions during flight. Therefore, this posture is probably derived from flight activities.

Head Lapping is, probably, derived from feeding behavior. Head Touching and Boxing, which involve the foretarsi, are probably derived either from feeding activities, since these species taste their food with their tarsi, or from preening activities.

The rejection responses of the female (kicking and preening-like movements) are also derived activities. Barber and Starnes (1949) mention that flies on a food source push other flies away with their middle and hindlegs. This activity is, most likely, the source of the kicking rejection responses of the females.

The response which was described as being similar to preening was probably derived from that activity.

The Genital Orientation and Genital Contact activities and positions are not believed to be derived. Activities for life sustaining functions are innate. The major function of adult flies is to reproduce;
1. Isolating mechanisms and their role in preventing hybridization of these species. The primary goal of the series of experiments dealing with hybridization of house fly and face fly was to determine if the two species would hybridize, and if not, what isolating mechanisms were active in preventing it.

Geographical isolation was overcome when face fly was introduced into North America. Seasonal isolation was not a factor, since, as the review of life history shows, both species are present in the field at the same time. Also, members of the various generations that are ready to mate, are present throughout the summer.

Habitat isolation may play a part in preventing hybridization of these two species in the field. However, the presence of house fly in the pasture and the presence of face fly near the barn are not uncommon. Thus, the two species do meet in each others' habitats, and there is a possibility of intermating. In the laboratory this isolating mechanism was overcome by placing the two species together.

Ethological isolation is partially effective in preventing hybridization. As Table X indicates, male house flies were far less successful in mating with female face flies than they were with their own species. The fact that the male house flies did mate with female house flies, and the male face flies did mate with the female face flies shows that all the flies were able and physiologically ready to mate. Therefore, the reduced success of the male house flies with female face flies must be due
to a behavioral difference between the males of the two species.

The fact that male face flies did not even attempt to mate with the female house fly is extremely interesting. The probable reason behind it will be discussed later.

Mechanical isolation evidently plays no part in the prevention of hybridization between male house fly and female face fly. Copulating females that were dissected within two hours after copula had sperm in their lateral sacs and/or spermathecae. These females dissected several days after copulation had no stored sperm, but a gelled substance was present. This gelled substance appeared to be similar to that described by Leahy and Craig (1967) in attempts to cross two species of mosquitoes of the same genus.

Since this gelled substance appears to be dead sperm and seminal fluid, the first effective isolating mechanism preventing hybridization between house fly and face fly appears to be gamete mortality. Sperm is transferred and follows the normal path from the lateral sacs to the spermathecae. The sperm, however, is not stored by the female of a different species. The death of the sperm may be due to an antigen type of reaction, or the sperm may not receive the proper nutrients for survival.

The presence of embryonated eggs in one experiment is difficult to explain. The number of embryonated eggs found was well within the limit of the number of eggs laid by one female. Female face flies do mate when their ovaries are fully developed (Miller and Treece, 1968). Therefore, the most logical explanation for the presence of embryonated eggs is that one female face fly mated with a male house fly when she was ready to oviposit and manure was available. The sperm was not stored,
but fertilized some of the eggs as they were laid.

Since none of the eggs in the same manure hatched, zygote mortality must have a role in preventing hybridization. Thus, in rare cases, when the timing is perfect, house fly may fertilize face fly eggs, but these eggs do not hatch.

Hybrid sterility and hybrid inferiority had no part in preventing hybridization between house fly and face fly, since no hybrids were produced.

2. *Wing damage in the hybridization experiments and its implications.* The observations of wing damage to male and female flies during the experiments on hybridization support the contention that female flies damage the wings of the male while rejecting courtship (cf. Table VIII and IX). The flies from the cages in which mating strikes were seen had far greater wing damage than those from other cages. It appears, then, that wing damage may be used as a criterion to determine mating attempts.

Using this criterion, the results of the male choice experiment demonstrate an interesting phenomenon.

Table I of the male choice experiment indicates that male house flies courted female face flies far more often than their own species. Table II shows that male face flies courted their own species more often than female house flies.

These results must be interpreted as the female face fly presenting an overoptimal stimulus to the male house fly, and the female house fly presenting a suboptimal stimulus to the male face fly. The question then arises as to the type of stimulus involved. As past research has demonstrated, the stimuli that elicit the strike are either visual (Vogel,
1957) or olfactory (Rogoff, 1964).

If the stimulus which caused the preference stated was olfactory, one would expect results similar to those of Shorey et al. (1965). That is, one female to elicit a normal level of response from her own species, and a higher level of response from the other species. The female of the other species would elicit a normal level of response from her own species, and a lower level from the other.

The male choice experiment provided results that could be compatible to those of Shorey et al. (1965). However, Rogoff et al. (1964) have demonstrated that extracts of female face fly do not stimulate male house fly to strike.

Visual stimuli, especially size, provide a more probable explanation. Female face flies are larger than female house flies. Thus, they provide an overoptimal visual stimulus to the male house fly. Conversely, female house flies are smaller than female face flies and provide a suboptimal visual stimulus to the male face fly. This may explain why no interspecific strikes were observed in cages of male face fly and female house fly.

The research concerning hybridization between house fly and face fly has raised several interesting questions:

1) Riemann and Thorson (1969) have demonstrated that the male accessory material of house fly that accompanies the sperm to the female stimulates oviposition and prevents second matings. The question raised is whether this material is species specific? Will the female face flies that have mated with male house flies remate with their own species?
Will these females lay eggs as readily as if they had mated conspecifically?

2) If male face flies do not mate with female house flies because of suboptimal stimuli, will small male face flies (produced by overcrowding the larvae) mate with female house flies? If they do, will these matings be fertile? In other words, if we overcome the premating isolating mechanisms that are effective in the field, will post-mating mechanisms come into play?

3) We have seen that wing damage can be used as an indicator of mating attempts. The question arises as to how definite an indicator it is. Perhaps the amount of wing damage can be correlated with the number of mating attempts. In this way, the attractiveness of a female could be measured accurately without time consuming, constant observation of flies.
VI. SUMMARY

The aims of this study included: Describing and comparing the courtship behavior of the house fly, *Musca domestica* L., and the face fly, *Musca autumnalis* De Geer; Analyzing the various activities of the courtship ritual and postulating their functions; and Attempting to hybridize these two species in the laboratory.

The techniques and materials utilized in rearing the insects, as well as the experimental techniques, were reported. A review of the life history, habits, and economic importance of the two species was presented. In addition, the literature concerning mating behavior, the functions and mechanisms of courtship, and courtship in Diptera was reviewed. Finally, the possible isolating mechanisms which may act as barriers to hybridization were described and discussed.

The courtship patterns of the house fly and the face fly were analyzed using slow motion photography and the individual elements that comprise the rituals were described. Similarities and differences in the courtship rituals of the two species were noted. Abnormal sexual behaviors and misdirected sexual activities were also reported.

Experimental hybridization of the two species was undertaken and the various isolating mechanisms that prevented successful hybridization were ascertained.

Analysis of the elements of courtship yielded information as to the possible functions and mechanisms of the courtships of these species. Comparison of the courtships revealed the slight differences in emphasis, form, and frequency that can be expected between closely related species.
Possible stimulus-response reactions in the courtships and possible derivations of the elements of the courtships were presented.

Finally, analysis of the degree of wing damage to the flies in the experimental hybridization yielded implications as to the usefulness of wing damage as a criterion for measuring mating attempts.
VII. CONCLUDING REMARKS

In a descriptive study such as this, one must be careful in stating unequivocally that certain conclusions which may be drawn are true. It is far more important that such a study provide the basis for posing questions and proposing hypotheses to answer these questions, since description is the basic step in achieving an understanding of any phenomenon.

The only unequivocal conclusions that can be drawn from this study are: 1. House fly and face fly perform a rigidly fixed, species-specific courtship pattern; 2. The patterns of these species are extremely similar; and 3. There are several isolating mechanisms which are active in preventing the hybridization of these species, especially ethological isolation and gamete mortality.

Other inferences and conclusions were presented during the discussion of the results of this study. The included proposed functions of the courtship elements, incompleteness of epigamic recognition, stimulus-response reactions in courtship, and the implications of wing damage to male and female flies.

The questions which arose from this study are numerous, and include:

1. What are the neurophysiological problems of the mechanisms of the stimulation of the female during courtship and are they species specific?

2. What is the function of the courtship of these species and the functions of the individual elements?

3. Is the male accessory material, which stimulates oviposition and
4. What are the roles of vision and olfaction in attracting males?

5. Is the female sex pheromone species specific?

6. How accurate is the degree of wing damage as an indicator of mating attempts?

Many other questions may be posed from the results of this study, and I hope that the review of the literature and the discussion of the results will stimulate many questions and provoke further research into the mechanisms and evolution of the courtship behavior in the genus *Musca.*
Figure 1.—Elements of the courtship of house fly.

A. Orientation

B. Landing : Wing vibration (continuous to F.)

C. Wing-Out : Leg-Up : Head Lapping

D. Wing-Out : Leg-Up : Head Lapping : Head Touching
Figure 1.-Elements of the courtship of house fly.

E. Wing-out : leg-up : Head Lapping: Boxing

F. Genital Orientation

G. Genital Contact

H. Copulation
Figure 2.—Elements of the courtship of face fly.

A. Orientation

B. Landing: Wing vibration (continuous to F.)

C. Fencing: Head Lapping

D. Fencing: Head Lapping: Head Touching
Figure 2.—Elements of the courtship of face fly.

E. Fencing : Head Lapping : Boxing
F. Genital Orientation
G. Genital Contact
H. Copulation
Figure 3.—Possible stimulus-response reactions in house fly courtship.

Suggested types of stimuli involved are presented in parentheses.
Male Reactions

Orientation (visual; olfactory)
\rightarrow Landing (contact chemoreception)
\rightarrow Wing vibration (tactile)
\rightarrow Leg-up (tactile)
\rightarrow Head Lapping (contact chemoreception)
\rightarrow Head Touching (tactile; contact chemoreception)
\rightarrow Boxing (contact chemoreception)
\rightarrow Backing
\rightarrow Genital Orientation (tactile)
\rightarrow Genital Contact
\rightarrow Copulation

Female Reactions

(olfactory; auditory)
\rightarrow Wing-out (?)
\rightarrow Raising Forelegs (tactile; contact chemoreception)
\rightarrow Extruding Ovipositor
Figure 4.—Possible stimulus-response reactions in face fly courtship.

Suggested types of stimuli involved are presented in parentheses.
Male Reactions

Orientation
   ↓
  (visual; olfactory)
Landing
   ↓
  (contact chemoreception)
Wing Vibration
   ↓
  (olfactory; auditory)
Fencing of Hindlegs
   ↓
   (tactile)
   (tactile; contact chemoreception)
Head Lapping
   ↓
  (contact chemoreception)
Head Touching
   ↓
   (tactile; contact chemoreception)
Boxing
   ↓
   (contact chemoreception)
Backing
Genital Orientation
   ↓
   (tactile)
Genital Contact
   ↓
   Copulation

Female Reactions

Fencing of Hindlegs
   →
  (tactile; contact chemoreception)

Raising Forelegs
   →
   (tactile; contact chemoreception)
Extruding Ovipositor
Table I.-The duration of the various life stages in the life history of house fly (H.F.) and face fly (F.F.).

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Hammer (1941)</td>
<td>10.5-23.0 hours(^a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Killough and McClellan (1969)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rockstein and Lieberman (1959)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Teskey (1969)</td>
<td>17 hr.*</td>
<td>3 days*</td>
<td>5 days*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>28 hr.**</td>
<td>8 days**</td>
<td>16 days**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treece (1965)</td>
<td>16 hr.***</td>
<td>4 days***</td>
<td>7-8 days***</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wang (1964)</td>
<td>20-23 hr.</td>
<td>3.5 days</td>
<td>7.5-8 days</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>West (1951)</td>
<td>8-12 hr.</td>
<td>5-16 days</td>
<td>5 days</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Values are for eggs laid in the A.M. and P.M., respectively
\(^\star\) At 30°C
\(^\star\star\) At 18°C
\(^\star\star\star\) At 27°C
\(^b\) Maximum for females.
\(^c\) Mean life expectancy for males.
\(^d\) Mean life expectancy for females.
Table II.-Various aspects of the reproductive biology of the house fly.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Nutrients essential for gametogenesis</th>
<th>Period of sexual maturation (hours)</th>
<th>Time spent in copula (min.)</th>
<th>Time for sperm transfer (min.)</th>
<th>Diurnal mating rhythm</th>
<th>Number of times adults will mate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chang (1965)</td>
<td>Sperm: 20-♂️ 40-♀️</td>
<td>50</td>
<td>as soon as copula begins</td>
<td></td>
<td></td>
<td>Male 1 Female 1</td>
</tr>
<tr>
<td>Hampton (1952)</td>
<td>Sperm: 90</td>
<td>90</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ilse and Mulherkar (1954)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>bimodal</td>
</tr>
<tr>
<td>Michelsen (1960)</td>
<td></td>
<td>18-20-♂️</td>
<td></td>
<td></td>
<td></td>
<td>none</td>
</tr>
<tr>
<td>Murvosh et al. (1964a)</td>
<td></td>
<td>16-♂️ 24-♀️</td>
<td>60</td>
<td>10</td>
<td>4-8</td>
<td></td>
</tr>
<tr>
<td>Sacca and Benetti (1958)</td>
<td></td>
<td>12-♂️ 72-♀️</td>
<td>84</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>West (1951)</td>
<td></td>
<td>Sperm: sugar protein</td>
<td>7/24 hr.</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zingrone et al. (1959)</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table III.-Various aspects of the reproductive biology of the face fly.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Nutrients essential for gametogenesis</th>
<th>Period of sexual maturation (hours)</th>
<th>Time spent in copula (min.) Average</th>
<th>Time for sperm transfer (min.)</th>
<th>Diurnal mating rhythm</th>
<th>Number of times adults will mate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Killough and McClellan (1969)</td>
<td>Sperm Egg</td>
<td>62</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lohda et al. (1970)</td>
<td>36-♂ 48-♀</td>
<td>66</td>
<td>6</td>
<td>unimodal</td>
<td>7-8/24 hr.</td>
<td></td>
</tr>
<tr>
<td>Teskey (1969)</td>
<td>48-♂ 72-♀</td>
<td>60-86</td>
<td></td>
<td>6-13</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Treece (1965)</td>
<td>48*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wang (1964)</td>
<td>sugar protein</td>
<td>96*</td>
<td>60</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* No mating was seen prior to this time.
Table IV.—Comparison of the time spent in various phases of courtship by male house flies and male face flies.

<table>
<thead>
<tr>
<th>Element</th>
<th>House fly</th>
<th>Time (seconds)</th>
<th>Face fly</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landing (L)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wing-out (W-O)*</td>
<td>1/16 - 2/16</td>
<td></td>
<td>1/16 - 2/16</td>
</tr>
<tr>
<td>Leg-up (L-U)*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head Lapping (HL)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head Touching (HT)</td>
<td>7/16 - 12/16</td>
<td></td>
<td>14/16 - 18/16</td>
</tr>
<tr>
<td>Boxing (B)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Backing (Ba)</td>
<td>8/16</td>
<td></td>
<td>8/16</td>
</tr>
<tr>
<td>Genital Orientation (GO)</td>
<td>1 8/16 - 3</td>
<td></td>
<td>20 - 30</td>
</tr>
<tr>
<td>Genital Contact (GC)</td>
<td>1 8/16 - 2</td>
<td></td>
<td>1 8/16 - 2</td>
</tr>
</tbody>
</table>

* House fly only.
Table V.—Comparison of the various elements of the courtship of house fly and face fly.

<table>
<thead>
<tr>
<th>Element</th>
<th>Presence</th>
<th>Face fly</th>
<th>Appearance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orientation (O)</td>
<td>+</td>
<td>+</td>
<td>S</td>
</tr>
<tr>
<td>Landing (L)</td>
<td>+</td>
<td>+</td>
<td>D</td>
</tr>
<tr>
<td>Wing-out (W-O)</td>
<td>+</td>
<td>-</td>
<td>D</td>
</tr>
<tr>
<td>Leg-up (L-U)</td>
<td>+</td>
<td>-*</td>
<td>D</td>
</tr>
<tr>
<td>Head Lapping (HL)</td>
<td>+</td>
<td>+</td>
<td>S</td>
</tr>
<tr>
<td>Head Touching (HT)</td>
<td>+</td>
<td>+</td>
<td>S</td>
</tr>
<tr>
<td>Boxing (B)</td>
<td>+</td>
<td>+</td>
<td>D***</td>
</tr>
<tr>
<td>Backing (Ba)</td>
<td>+</td>
<td>+</td>
<td>S</td>
</tr>
<tr>
<td>Genital Orientation (GO)</td>
<td>+</td>
<td>+</td>
<td>S</td>
</tr>
<tr>
<td>Genital Contact (GC)</td>
<td>+</td>
<td>+</td>
<td>S</td>
</tr>
<tr>
<td>Forward (F)</td>
<td>+</td>
<td>-**</td>
<td>D</td>
</tr>
<tr>
<td>Copulation (C)</td>
<td>+</td>
<td>+</td>
<td>S</td>
</tr>
</tbody>
</table>

+ Indicates present.  
- Indicates absent.  
S Indicates similarity of appearance.  
D Indicates difference of appearance.

* Modified to fencing.  
** Uncommon, but was observed.  
*** Position of male’s body differs.
Table VI.-The degree of wing damage to the five female face flies, one female house fly, and five male house flies confined together in cages A₁ and A₂ of the male choice experiment.

<table>
<thead>
<tr>
<th>Specimen number, sex, and species</th>
<th>Cage A₁</th>
<th>Cage A₂</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Right wing</td>
<td>Left wing</td>
</tr>
<tr>
<td>1. Female face fly</td>
<td>1/2 missing</td>
<td>tip ripped</td>
</tr>
<tr>
<td>2. Female face fly</td>
<td>2/3 missing</td>
<td>tip ripped</td>
</tr>
<tr>
<td>3. Female face fly</td>
<td>1/3 missing</td>
<td>2/3 missing</td>
</tr>
<tr>
<td>4. Female face fly</td>
<td>1/2 missing</td>
<td>tip ripped</td>
</tr>
<tr>
<td>5. Female face fly</td>
<td>1/3 missing</td>
<td>tip ripped</td>
</tr>
<tr>
<td>6. FEMALE HOUSE FLY</td>
<td>NORMAL</td>
<td>NORMAL</td>
</tr>
<tr>
<td>7. Male house fly</td>
<td>2/3 missing</td>
<td>2/3 missing</td>
</tr>
<tr>
<td>8. Male house fly</td>
<td>normal</td>
<td>normal</td>
</tr>
<tr>
<td>9. Male house fly</td>
<td>3/4 missing</td>
<td>tip ripped</td>
</tr>
<tr>
<td>10. Male house fly</td>
<td>tip ripped</td>
<td>3/4 missing</td>
</tr>
<tr>
<td>11. Male house fly</td>
<td>3/4 missing</td>
<td>1/3 missing</td>
</tr>
<tr>
<td>Specimen number, sex, and species</td>
<td>Cage B₁</td>
<td>Cage B₂</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>---------</td>
<td>---------</td>
</tr>
<tr>
<td>1. Female house fly</td>
<td>normal</td>
<td>normal</td>
</tr>
<tr>
<td>2. Female house fly</td>
<td>normal</td>
<td>normal</td>
</tr>
<tr>
<td>3. Female house fly</td>
<td>normal</td>
<td>normal</td>
</tr>
<tr>
<td>4. Female house fly</td>
<td>tip ripped</td>
<td>tip ripped</td>
</tr>
<tr>
<td>5. Female house fly</td>
<td>tip ripped</td>
<td>normal</td>
</tr>
<tr>
<td>6. FEMALE FACE FLY</td>
<td>TIP MISSING</td>
<td>1/3 MISSING</td>
</tr>
<tr>
<td>7. Male face fly</td>
<td>1/3 missing</td>
<td>2/3 missing</td>
</tr>
<tr>
<td>8. Male face fly</td>
<td>1/3 missing</td>
<td>1/3 missing</td>
</tr>
<tr>
<td>9. Male face fly</td>
<td>tip ripped</td>
<td>tip ripped</td>
</tr>
<tr>
<td>10. Male face fly</td>
<td>tip ripped</td>
<td>tip ripped</td>
</tr>
<tr>
<td>11. Male face fly</td>
<td>--------*</td>
<td>--------*</td>
</tr>
</tbody>
</table>

* Died
Table VIII.-Summary of the various aspects of the experimental hybridization of female face flies and male house flies.

<table>
<thead>
<tr>
<th>Test number</th>
<th>Attempted copulation</th>
<th>Successful copulation</th>
<th>Sperm in female</th>
<th>Male wings broken</th>
<th>Female wings broken</th>
<th>Embryo in eggs</th>
<th>Eggs hatched (larvae or pupae found)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>2.</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>3.</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>+**</td>
</tr>
<tr>
<td>4.</td>
<td>+</td>
<td>+</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>5.</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6.</td>
<td>+</td>
<td>+</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>X</td>
<td>-</td>
</tr>
</tbody>
</table>

+ Denotes positive results.
- Denotes negative results.
X Denotes that no examination was made.
* Within one hour after copulation.
** Due to contamination by female house flies.
*** Copulation was observed several hours prior to the dissection.
Table IX.—Summary of the various aspects of the experimental hybridization of female house flies and male face flies.

<table>
<thead>
<tr>
<th>Test number</th>
<th>Attempted copulation</th>
<th>Successful copulation</th>
<th>Sperm in female</th>
<th>Male wings broken</th>
<th>Female wings broken</th>
<th>Embryo in eggs</th>
<th>Eggs hatched (larvae or pupae found)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>-</td>
<td>-</td>
<td>X</td>
<td>-</td>
<td>-</td>
<td>X</td>
<td>-</td>
</tr>
<tr>
<td>2.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>3.</td>
<td>-</td>
<td>-</td>
<td>X</td>
<td>-</td>
<td>-</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>4.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>5.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>6.</td>
<td>+*</td>
<td>+*</td>
<td>-**</td>
<td>+</td>
<td>-***</td>
<td>X</td>
<td>-***</td>
</tr>
</tbody>
</table>

+ Denotes positive results.
- Denotes negative results.
X Denotes that no examination was made.

* Cage was contaminated with one female face fly.
** Refers to female house flies only—the female face fly had sperm and only stubs of wings.
*** The eggs that hatched developed into face fly pupae—they were from the female face fly.
Table X.-The relative success of male house flies in overcoming ethological isolation.

<table>
<thead>
<tr>
<th>Combination and pair number</th>
<th>Time before copulation (min.)</th>
<th>Duration of copulation (min.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>House fly 1.</td>
<td>5</td>
<td>71</td>
</tr>
<tr>
<td>X 2.</td>
<td>5</td>
<td>65</td>
</tr>
<tr>
<td>House fly 3.</td>
<td>7</td>
<td>56</td>
</tr>
<tr>
<td>4.</td>
<td>7</td>
<td>70</td>
</tr>
<tr>
<td>5.</td>
<td>78</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>$\bar{x}$ 20.4</td>
<td>$\bar{x}$ 64.4</td>
</tr>
<tr>
<td>Face fly 1.</td>
<td>14</td>
<td>63</td>
</tr>
<tr>
<td>X 2.</td>
<td>61</td>
<td>74</td>
</tr>
<tr>
<td>Face fly 3.</td>
<td>95</td>
<td>66</td>
</tr>
<tr>
<td>4.</td>
<td>185</td>
<td>35</td>
</tr>
<tr>
<td>5.</td>
<td>290</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>$\bar{x}$ 129</td>
<td>$\bar{x}$ 55</td>
</tr>
<tr>
<td>Male 1.</td>
<td>140</td>
<td>30</td>
</tr>
<tr>
<td>House fly 2.</td>
<td>298</td>
<td>32</td>
</tr>
<tr>
<td>X 3.</td>
<td>---</td>
<td>53*</td>
</tr>
<tr>
<td>Female 4.</td>
<td>---</td>
<td>42*</td>
</tr>
<tr>
<td>Face fly 5.</td>
<td>---</td>
<td>64*</td>
</tr>
<tr>
<td></td>
<td>$\bar{x}$ 212</td>
<td>$\bar{x}$ 37.5</td>
</tr>
<tr>
<td>Male 1.</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>Face fly 2.</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>X 3.</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>Female 4.</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td>House fly 5.</td>
<td>---</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\bar{x}$ ---</td>
<td>$\bar{x}$ ---</td>
</tr>
</tbody>
</table>

* Denotes data from another experiment.
Table XI.—Elements common to the courtship of some Diptera.

<table>
<thead>
<tr>
<th>Insect and reference</th>
<th>Touching foretarsi vibration</th>
<th>Male wing legs (not raised)</th>
<th>Female legs of female</th>
<th>Immobilize hindlegs</th>
<th>Wing-out position of hindlegs</th>
<th>Male licks body of female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tipulidae</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Tipula oleracea</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stich (1963)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Culicidae</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aedes aegypti</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roth (1948)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tephritidae</td>
<td></td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td>Tauber and Toschi (1965)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drosophilidae</td>
<td></td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td>+</td>
</tr>
<tr>
<td><em>Drosophila sp.</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Speith (1952)</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Muscidae</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
</tr>
<tr>
<td><em>Fannia sp.</em></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Tauber (1968)</td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td><em>Musca domestica</em></td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Present study</td>
<td></td>
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</tr>
<tr>
<td><em>Musca autumnalis</em></td>
<td></td>
<td>+</td>
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<tr>
<td>Present study</td>
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<td></td>
</tr>
<tr>
<td>Calliphoridae</td>
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<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>+</td>
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<tr>
<td><em>Lucilla cuprina</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bartell et al. (1968)</td>
<td></td>
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</tbody>
</table>


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