

# STUDIES ON THE MATING BEHAVIOR OF THE HOUSE FLY, *MUSCA DOMESTICA* L.<sup>1</sup>

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Fundamental knowledge on the mating behavior of insects is more important today than ever, not only because of academic interest, but also because of recent advances by means of which control or eradication of pest species is possible through sterilization by radiation and/or chemicals. Although investigators have studied the house fly for many years, surprising gaps exist in our knowledge of the basic biology of this species. House fly mating behavior has been previously described in rather general terms, but only a few detailed investigations have been reported in the literature. The research presented herein was conducted to add to this fund of necessary information and represents an attempt to elucidate certain aspects of mating behavior.

The Orlando regular house fly colony, a laboratory strain 20 years old, was used in performing these studies.

## INITIAL MATING AGE

Two series of tests were run to determine the age at which male and female flies would mate with a successful transfer of motile sperm. In the first series, five sexually mature males, 72 hr old were anesthetized with carbon dioxide, allowed to recover, and then confined for 2 hr in each of a series of cages (10×8×10 inches) containing five virgin females: 4, 6, 16, 20, 24, 26, 28, 30, or 48 hr old. The females were then anesthetized with carbon dioxide and the spermathecae excised and examined for motile sperm by the method of Sacca (1957). In the second series, the approach was reversed in that five mature females were introduced into cages containing males of various age groups. Insemination was determined as in the previous series. Tests with each age group were replicated five times so that a total of 25 flies of each sex for each age group was observed.

Mature males inseminated no females 4 to 26 hr old, but inseminated 40 per cent of the females that were 28 hr old, 56 per cent of those 30 hr old, and 80 per cent of those 48 hr old. No mature females were inseminated by males 4, 6, or 16 hr old; but 8 per cent were inseminated by males 20 hr old, 12 per cent by males 24 hr old, and 88 per cent by males 26 hr old. In four of the tests, one each with males 6, 20, 24, and 26 hr old, mating was in progress when the flies were anesthetized; but upon dissection of the spermathecae no sperm were found in any of the females.

These results indicate that males and females will not mate for at least 16 and 24 hours, respectively, after emergence. Anesthesia prior to mating may have retarded the process somewhat, but this factor was not measured. Michelsen (1960), who did not anesthetize the flies prior to mating, reported that males, at 28 C, reached sexual maturity in 18 to 27 hr after emergence. This finding was consistent with the results of our tests.

## THE MATING STRIKE

Observations of precopulatory behavior were conducted to define more accurately the events that occur. The flies were observed in screen cages (10×8×10 inches) and in a small (6×6×2 inches) wooden cage covered on two sides

<sup>1</sup>Manuscript received August 24, 1963.

by 6-inch glass plates. A 2-power magnifying glass was used to watch the flies in the smaller cage. The basic sequence of events is given below.

The male approaches the female from any direction, e.g., head on or from the side, but usually from the rear. The seizure, or mating "strike," may start while one or both are in flight but it ordinarily occurs while both are resting or walking on some surface. The word "strike" is synonymous with "jump," as used by Ilse and Mulherkar (1954), but seems more appropriate since "jump" does not accurately describe what occurs during aerial contact. Hewitt (1914) refers to the strike as "a carefully calculated leap from a short distance." Our observations neither confirmed nor disproved this definition.

If the strike does occur in mid-air, both flies immediately fall to some surface. Copulation never occurs in the air; but sometimes, if disturbed, a copulating pair may leave one surface and fly quickly to another. The female may avoid the strike by flying or darting away; but, if the strike is successful, the male usually lands on the dorsum of the thorax facing the same direction as the female. However, a few males were seen to land facing in the opposite direction, then quickly reversed themselves. As the male is approaching and about to make contact, his tarsi often appear to hit the wing of the female in the region between the apical and anal area; but this action is very difficult to see because of the swift movement.

When the actual seizure or strike occurs, the prothoracic and mesothoracic tarsi of the male are placed on the base of the female's wings while the metathoracic legs are beneath her abdomen at the base of the wings. Instantaneously, the wings of the female extend into horizontal flight position and vibrate rapidly. Her metathoracic legs are usually lifted into the air and placed under her wings as though supporting them. The metathoracic legs of the male, which are beneath the base of her wings, appear to operate as a lever lifting them. The outward movement of the female's wings may be due to a combination of factors, but the main cause appears to be pressure exerted by the metathoracic legs of the male. Evidence was obtained to support this assumption. When the metathoracic legs of the male are amputated, he has a difficult time seizing the female and is not as successful in forcing her wings out. At times he can do so by placing his mesothoracic legs beneath her wings. Amputation of the male's metathoracic legs does not completely prevent successful mating, but it does retard the process. When mature male amputees were caged with mature virgin females, little mating took place for 1 to 2 days, but after 5 days most of the females became inseminated.

Males often strike other males, as described in another section of this paper, but rarely are the wings extended by the assaulted males. A male-to-male strike usually requires about  $\frac{1}{2}$  second and is then terminated. In females, vibration of wings is often accompanied by a loud buzzing sound. Some females produced this sound even with the wings held immobile on adhesive tape, although the buzz was not as loud. The calypters, however, were free to vibrate and they may have produced the sound.

The male now reaches forward and strokes or "caresses" the head of the female with his prothoracic legs, which have been moved from their position on the wing base. It should be kept in mind that this reaching forward by the male occurs simultaneously with the outward movement of the female's wings. Some pressure appears to be exerted, for the female's head is forced down. The wings of the female are still extended and only the mesothoracic tarsi of the male rest at her wing base. At times it appears that the male uses his head to "nuzzle" the head of the female, but this action is difficult to see since the flies are in constant motion. The female, if previously mated, may struggle violently to throw the male off.

The male now moves toward the rear of the female, placing the ventral part of his abdomen against her dorsal abdominal segments. Part of the male's abdo-

men projects beyond the tip of the abdomen of the female. The prothoracic tarsi of the male, formerly stroking the head of the female, now rest on the thorax of the female, but may lie at the base of the wings or even on the wings of the female. The mesothoracic legs have moved from the thoracic area and now rest alongside the female's abdomen or may rest on or over her wings. The metathoracic tarsi are wrapped beneath the female's abdomen on the ventral surface and may or may not be folded crosswise. Both Hewitt (1914) and West (1951) stated that the legs are folded crosswise but our observations showed that the male's legs were not always in this position. The female's wings now lie in the normal position along her abdomen.

One of the following then occurs:

(a) The female, if a virgin, accepts the male and thrusts her ovipositor into the genital opening of the male. The copulatory position, with the male above, is called "superimposed" by Hardy (1944).

(b) The female may be passive throughout the strike and not accept the male. He quickly leaves and may or may not strike again. One male was seen striking and leaving the same female six consecutive times.

(c) The female struggles throughout most of the strike and finally drives the male away by shaking him off. Actually the male may be forced off at any time throughout the strike and at times he appears to leave voluntarily.

The situations described in (b) and (c) normally occur with females that have already mated. The total elapsed time for a strike usually ranges from 1 to 9 seconds and averages about 3 seconds; but if the strike results in copulation, the flies remain coupled for a much longer period as noted later in this paper. This procedure has been described in an arbitrary stepwise fashion but actually occurs as a continuum.

#### COPULATION TIME

Tests were run to determine the actual time house flies remained in coitu after initial seizure. A 7-day-old virgin male was put into a cage containing virgin females of the same age. Immediately after the initiation of copulation, the time was noted and the mating flies were trapped in a plastic vial and set aside unmolested. Mating pairs that uncoupled during the transfer were discarded. As soon as copulation was terminated and the insects disengaged, the time was recorded. Of 61 mating pairs that were trapped and observed, the shortest mating period was 44 min, whereas the longest extended to 96 min. The average time was 60 min. Hampton (1952), on the basis of more than 50 observations, stated that copulation lasts longer than 30 min, and may last 2 hr, but that the usual time is 1½ hr. Sacca and Benetti (1960) reported, from 110 observations, a mean of 84 min, a maximum of 136 min and a minimum of 59 min.

A test was then run to determine whether the length of time house flies remained in coitu affected the degree of insemination, that is, the extent to which each of the three spermathecae of a female was filled with sperm. Virgin 7-day-old male and female flies were allowed to copulate for periods ranging from 1 to 76 min and then anesthetized and separated. The spermathecae were then excised and examined for sperm.

The results of this experiment are given in table 1. After mating periods of 1 and 2 min, no sperm were found in the females, but after 3 to 5 min, some spermathecae contained a few sperm and some were completely filled. These results differed from those given in the classical texts. Hewitt (1914) stated that the whole act may be over in a few moments or the sexes may remain in coitu for several minutes, but West (1951) indicated that the act requires from a few seconds to several minutes. No clear distinction is made between the act of copulation and the act of sperm transfer. As we have shown, the copulatory act often lasts an hour or more but complete sperm transfer seems to require 10

min or less. Although our sample size was small, indications were that sperm transfer does not occur during the first 2 minutes. When the flies remained in coitu for periods of 10 to 76 min, the spermathecae were filled to capacity except in one instance at the 20-min period when only one spermatheca was filled.

TABLE 1  
*Relationship between the length of time virgin 7-day-old house flies remained in copulation and the degree of insemination*

Time in copulation (min)	Number of replications	Number of spermathecae with sperm
1	4	0
2	3	0
3	1	3 <sup>a</sup>
3	2	0
4	2	0
4	1	3 <sup>b</sup>
5	1	3
5	1	0
10	2	3
15	2	3
20	1	1
20	1	3
25	2	3
30	2	3
51	1	3
54	1	3
59	1	3
61	1	3
64	1	3
68	1	3
72	2	3
76	1	3

<sup>a</sup>Very few sperm.

<sup>b</sup>Two heavily filled, one lightly filled.

#### SEX RECOGNITION

Studies were made on mating behavior to establish whether sex recognition was evident in the house fly, since observations indicated that males attempted to mate with other males as well as females.

Fifty virgin males were anesthetized with carbon dioxide, tagged on the thorax with opaque white drawing ink, and put into a cage with 50 virgin females. Records were then made of the number of times that a marked male tried to mate with another marked male as compared with the number of mating strikes made at a female. Broadly defined, a "strike" occurs when a male seizes a female at the base of the wings, forcing them out into horizontal flight position, and strives to copulate. Measurements of 47 male strikes at females averaged 3 sec each, with a range of 0.5 to 9 sec. When a male strikes at another male, the time is shorter (usually 0.5 sec or less) because he cannot force the wings out and the strike ends abruptly. In the following studies, the numbers of strikes during 15-min observation periods were recorded. The first set of observations was made with flies 4 and 5 days old. The numbers of strikes per 15-min observation period with females and with other males are shown in table 2.

A second group of observations was made on two cages of flies, each containing 50 virgin males and 50 virgin females, 2, 3, 4, 5, 8, 9, 11, or 12 days old. The

thorax of each male was marked with orange artist's pigment (powdered tempera dissolved in a mixture of shellac in alcohol). Table 3 contains the results showing the number of daily observations for each age group and the mean number of strikes per 15-min observation period.

In view of the number of times that males attempt to mate with other males, it seems justifiable to assume that only incomplete sex recognition exists on the part of the male house fly. This assumption is supported by other observations during which males were seen to strike at dead males and females as well as pupal

TABLE 2  
*The number of mating strikes by male house flies at females  
and at other males\**

Time observed		With females	With males
July 30	8:00 AM	47	22
	9:45 AM	33	7
	10:45 AM	40	27
	12:45 PM	45	19
	3:00 PM	51	20
July 31	8:00 AM	30	10
	10:45 AM	44	8
	4:00 PM	42	5

\*Each datum represents a 15-min observation of 50 flies of each sex, caged when 4 or 5 days old.

TABLE 3  
*The number of mating strikes by male house flies of different ages at female  
flies and at other males\**

Age of flies (days)	No. of 15-min observations per day	Strikes with females (Mean/15-min observation period)	Strikes with males (Mean/15-min observation period)
2	6	6.1	1.1
3	6	33.1	12.1
4	8	34.8	16.3
5	6	37.0	16.5
8	6	18.3	9.1
9	3	18.0	6.3
10	1	20.0	1.0
11	2	10.5	6.0
12	2	13.5	4.0

\*These data show the number of observations in a day and the mean number of strikes per 15-minute observation period.

cases lying on the floor of the cage. This behavior was uncommon, but not rare. Males also have been observed attempting a strike at another male that was trying to copulate with a female, and at other times trying to strike the female beneath the male. Males were observed making consecutive strikes at the same fly, e.g., striking, leaving, and striking again, regardless of sex. The female never tried to initiate mating.

There were relatively few successful copulations considering the number of

strikes. Usually only one or two pairs of flies could be seen in coitu during each 15-min observation period but, as noted in a previous section of this report, most females were observed to mate during the first few days after emergence and few females mate more than once, as reported by Zingrone et al. (1959). Fewer strikes were made by males older than 8 days but this observation did not necessarily indicate a diminishing mating drive after this age since some of the flies in the cage had died. Half the flies remained alive on the eleventh day after caging. The male sex drive remained strong, suggesting that the sex drive is not dependent upon or altered by the presence of mated or virgin females.

It appears that male house flies cannot invariably distinguish between a male or female, whether alive or dead, assuming that the strike, as defined, constitutes a definite mating attempt. However, the higher number of strikes at females seemed to indicate some degree of sex recognition.

The stimulus that initiates a strike was not identified. It may be visual, but preliminary tests have shown that flies mated successfully in dark cages (10×8×10 inches) when 25, 50, or 100 flies were confined to each cage.

#### MATING BEHAVIOR OF HOUSE FLIES IN A FEMALE-FREE ENVIRONMENT

A study was made of the mating behavior of male flies in a female-free environment to gain information on the requirement for an attractant or stimulant pro-

TABLE 4  
*Mating activity of flies in a female-free environment\**

Age of flies (days)	Cage No. 1		Cage No. 2	
	Time observed	No. of strikes/15 min	Time observed	No. of strikes/15 min
1	1:30 PM	0	1:15 PM	0
	3:45 PM	0	3:30 PM	0
2	8:45 AM	13	8:30 AM	4
	11:00 AM	10	11:15 AM	6
3	3:15 PM	13	3:45 PM	10
	12:30 PM	14	1:00 PM	3
4	3:45 PM	11	4:00 PM	13
	8:45 AM	8	9:15 AM	4
5	1:00 PM	12	12:45 PM	0
	2:45 PM	11	3:00 PM	3
	4:00 PM <sup>a</sup>	12	4:15 PM <sup>a</sup>	4

\*The figures represent the number of times that males tried to mate with other males (50 virgin males per cage).

<sup>a</sup>A small cage of several hundred mixed males and females placed inside both larger cages at 3:15 PM.

duced by females as a prerequisite to mating strikes by males. Two metal cages (10×8×10 inches) were washed with detergent, rinsed in acetone, and decontaminated in an oven for 12 hr at 300 F. The cages were covered with new cheesecloth. Fifty virgin males were collected as they emerged from pupal cases and placed in cage No. 1. This cage was put into a room that was free of flies and had never been used for studies on house flies. Fifty additional virgin males were anesthetized with carbon dioxide, separated from virgin females about 1 hr after emergence, and placed in cage No. 2. This cage was placed in a building in which flies had never been colonized. Eleven 15-min observations of mating attempts or strikes were made of each cage during a 5-day period. At the end of the fifth day, a small cage containing several hundred mixed males

and females of different ages was placed inside each of the two larger cages to see whether any change in activity would occur. The flies in each smaller cage did not come into direct contact with the males in the larger cage. Table 4 gives the number of observed mating attempts.

Very little activity was observed on the day of emergence. The flies usually remained motionless on the sides of the cage, doing little more than rubbing their tarsi. Few fed or took water. Likewise, little flight activity occurred even though they were capable of strong flight. Activity began to increase by late afternoon, but mating strikes were not seen until the second day. On this day virgin males definitely tried to mate with other males, even in the cage completely isolated from females or a female scent from the time of emergence. Males made a few strikes at a pupal case that was put into the cage. No increase in activity was observed during the 45 min after a small cage of mixed males and females was introduced into each of the larger cages. These results provided evidence that no sex attractant or copulation stimulant produced exclusively by female house flies is required to induce mating strikes by males, but did not disprove the existence of such an attractant or stimulant.

#### MATING ACTIVITY OF MALES AS AFFECTED BY THE PRESENCE OF MATURE FEMALES

Initial mating-age studies showed that males and females do not mate for about 16 and 24 hr, respectively; but no indication was given as to whether they attempted to mate prior to this period. Observations of males in a female-free environment confirmed that they try to mate with each other on the second day

TABLE 5

*The mating activity of newly emerged virgin male flies caged with mature 4-day-old virgin females (Cage No. 1) and of mature 4-day-old virgin males caged with newly emerged virgin females (Cage No. 2)\**

Time observed	Number of strikes	
	With females	with males
	Cage No. 1	
12:45 PM	0	0
3:00 PM	0	0
	Cage No. 2	
1:00 PM	5	7
3:15 PM	12	12

\*50 flies of each sex per cage.

after emergence and thereafter but that the mating drive is absent during most of the day of emergence. The question then arose as to whether newly emerged males would exhibit a mating response if they were caged with mature females.

A test was then conducted to determine whether the inactivity of males on the day of emergence was affected by the presence of mature females. Fifty newly emerged virgin males and fifty 4-day-old virgin females were put into cage No. 1. Fifty 4-day-old virgin males were put into cage No. 2 with 50 newly emerged virgin females. The males in both cages were marked by dusting with U. S. Radium Corp. No. 2200 blue-white fluorescent dust.<sup>2</sup> Observations were made under ultraviolet light for 15-min periods. Behavior appeared the same under ultraviolet light as under normal light. The test was set up at 8:00 AM.

As indicated in table 5, the males in cage No. 1 did not try to mate, but the

<sup>2</sup>U. S. Radium Corporation, Morristown, New Jersey. Mention of this company does not necessarily imply endorsement of its product by the U. S. Department of Agriculture.

males in cage No. 2 reacted normally, trying to mate with both males and females. Newly emerged males apparently required about a day to mature sexually. The inactivity of males on the day of emergence was not affected by the presence of mature females.

#### SEX ATTRACTION

Dramatic examples of sex attraction are found among certain insects such as the Silkworm Moth, *Bombyx mori* (L.); the Gypsy Moth, *Porthetria dispar* (L.); and the American Cockroach, *Periplaneta americana* (L.). The female Gypsy Moth, for example, emits an odor that is capable of attracting large numbers of males. The first indication of any such mechanism in the house fly apparently was found in 1962 at the Division's laboratory in Corvallis, Oregon. Rogoff et al. (1963) recently reported on this work.

The results of our experiments with sex attraction at Orlando, during the latter part of 1962, also demonstrated evidence of a similar nature, even though the tests were performed by a somewhat different procedure. Our experimental procedure has not been completely standardized and detailed results will be given in a later paper. Preliminary tests, thus far, have indicated that virgin males do not attract other virgin males. Young virgin females (1 to 24 hr old) attracted few or no males; whereas 7-day-old virgin females, whether alive or freshly killed, consistently attracted a small percentage of virgin males. The results, although consistent, are of a low order and not as striking as the attraction demonstrated by certain moths.

#### SUMMARY

The mating behavior of the house fly is a complex phenomenon involving several factors: (1) Both males and females must undergo a sexual maturation time of about one day before mating occurs. (2) The male apparently has an instinctive drive to mate, not dependent upon the presence of the female or a female odor. (3) Males will attempt copulative strikes with males or certain inanimate objects but strike more readily and frequently at females. (4) Preliminary evidence suggests the presence of some type of a female sex attractant of a low order.

That some type of female sex attractant is present and that males cannot differentiate between sexes are not necessarily two incompatible ideas as long as sex recognition is not taken to mean an exact recognition of the female as such. Imperfect sex recognition in the male combined with a low-order sex attractant in the female would explain why males attempt to mate with either sex and also why the higher ratio of male-to-female strikes occurs.

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