

REPRODUCTIVE BEHAVIOR OF THE SPIDER

1.

MECYANOGEA LEMNISCATA

A Thesis

Presented to

The Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of
Master of Arts

by

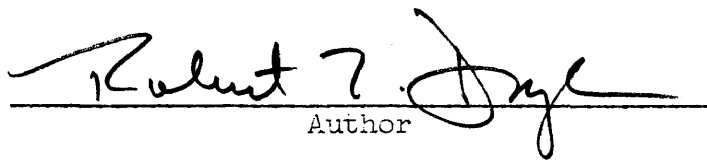
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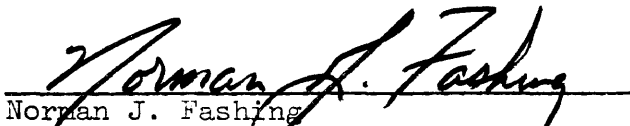
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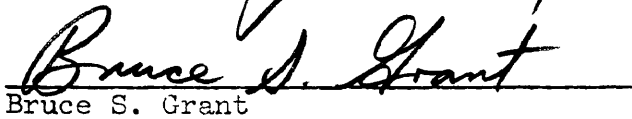


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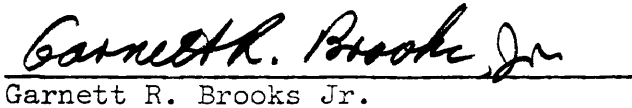
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ABSTRACT

The reproductive behavior of Mecyanogea lemniscata is investigated.

Sperm induction by the male consists of sperm web construction (with thread plucking), ejaculation and palpal application to charge the organs.

Courtship in this species is broken down into two parts: introductory courtship and epithalamic courtship. Introductory courtship consists of three types: 1) matrix plucking; 2) peripheral dome strumming and 3) charging. As such, introductory courtship functions to facilitate the male's entry to the female's dome.

The courtship releaser system of M. lemniscata displays a latitude of response and may be abbreviated while the male and female are cohabiting. The male appears to be in no danger during courtship and copulation. The male utilizes his legs to manipulate the female's abdomen to assure palpal insertion. Insemination of the female is also aided by the fact that a pair may cohabit for up to six weeks during which time they may copulate repeatedly.

The female becomes sexually unresponsive once she begins to produce eggcases. Females produce from one to nine eggcases each containing approximately fifteen eggs. Some eggcases are parasitized by an unidentified scelionid wasp.

It is suggested that the specimens observed are comprised of two behavioral phenotypes or come from two sibling species. Behavior modifications are examined relative to web structure and possible parasite defenses are discussed.

REPRODUCTIVE BEHAVIOR OF THE SPIDER

MECYANOGEA LEMNISCATA

INTRODUCTION

Many studies have been conducted on the sexual behavior of spiders, and it has been found that sexual behavior corresponds to their ecology and dominant senses. Platnick (1971) categorized the known patterns of spider courtship into three groupings which are dependent upon the prime releaser of the male display: 1) direct contact with the female, 2) chemoperception of a pheromone of the female, and 3) sight of the female. Within each group, the behavior of a particular species during the mating season is modified and defined by that species' particular life style.

Level one of Platnick's system is occupied by some mygalomorphs (tarantulas and trap door spiders), haplogynes (Dysdera; Loxosceles - the brown recluse) and most of the clubionid-thomisid line (the sac spiders and the crab spiders). Most thomisids (crab spiders) capture prey by first making physical contact and then quickly pouncing on it. Similar behavior is also noted in mating. For example, in Tibellus oblongus the partners are entirely unaware of each other until they physically touch. Upon contact, the male immediately seizes one of the female's legs and holds her for thirty to sixty seconds. Upon release of the leg, the female assumes the copulatory position. The male then ties her down with silk and copulation proceeds, after which the male leaves the female to free herself from her bonds (Kaston 1936).

Platnick (1971) places the genus Sicarius (desert spider) in category two; however, Levi (1967) studied the mating behavior in this genus and did not find chemoperception utilized in locating the female. Courtship did not begin until the male touched the female, therefore Sicarius belongs in category one of Platnick. Sicarius inhabits arid and desert areas where they bury themselves in the sand, and courtship begins when the male touches the partly exposed abdomen of the female. He digs her out of the sand and they stand face to face. After tactile movements by the male, copulation is accomplished with the male inserting both palpi simultaneously. The eggsac of this species, which also reflects its life style, is made of sand grains and resembles a mud dauber's nest (Levi 1969).

Intermediate between levels one and two, Platnick places some of the Lycosidae (wolf spiders) and Pisauridae (nursery web weavers). Pisaurids are wandering spiders (Comstock 1967) which stalk their prey. Pisaura mirabilis males wrap prey and carry it in their jaws until a female is found. The male mates with the female when she begins feeding on the wrapped prey (Bristowe and Locket 1926). Male Dolomedes wait until a female is feeding and then mate with her (Platnick 1971). Female Pisaurids carry their large eggcases around with them as they wander (Comstock 1967).

Although Platnick places lycosids between level one and two, there is evidence that sight is also greatly utilized by this group for mating. In addition, some lycosids use auditory communication (Hallander 1967, Rovner 1967) although it is not the prime releaser of the male display. Kaston (1936) reported on the mating behavior

of ten lycosid species. Four of these used touch as the prime releaser, five of them used sight or chemoperception, and one species seemed to utilize sight exclusively. The percussive behavior of selected lycosids is of interest in terms of mating behavior correlated to life style. Both Lycosa gulosa and Lycosa chelata employ drumming in the initial phase of courtship (Hallander 1967). In order to perceive the male's drumming, the female must stand on a substratum which will easily conduct the vibrations. These species have an attraction to dry leaves in the springtime, which transmit vibrations readily.

Using pheromonal cues, groups which comprise level two are extremely varied. Most notable of these are the web builders. Modification of sexual behavior due to adaption to life in a silken web is remarkable. Spiders possessing this style of living have highly developed tactile senses.

In the Agelenidae the males wander in search of a female in autumn (Comstock 1967), upon finding the web of a female the male taps on the very dense sheet web (funnel web weavers) and waits for her to assume the mating position. He then carries her into the funnel where copulation takes place (Montgomery 1910). At least one agelenid is an exception to this basic pattern. Argyroneta aquatica, the Urasian water-spider, lives underwater. Air bubbles adhere to the many body hairs of this species and are used to construct an air bell. The spider builds a loose horizontal web underwater and air bubbles are trapped by the web when the spider brushes them from the abdominal hairs. The spider makes several

trips to the surface to carry more air bubbles down to the growing air bell. Courtship and mating take place underwater inside the air bell. The male constructs a smaller bell for his sperm web and the female also fabricates another bell for her eggs (Kaestner 1963).

The orb weavers (Araneidae, Theridiosmatidae and Tetragnathidae) display a communication of utmost interest. The male approach is, in general, slow and highlighted by the male vibrating the threads of the female's web in a species-specific manner. Various authors have used different terms to describe this web vibration: "tweak" (Platnick 1971); "pulls", (Locket and Bristowe 1926); "glucks", (Blanke 1973); and "twang", (Mascord 1966). Thread vibrations are perpetrated in different locations depending on the web of the species. A Gasteracantha minax male twangs a radius of the female's web as the female rests in the center of the orb (Mascord 1966). This behavior is also seen in Araneus diadematus (Witt 1975). With Zilla x-notata, the female hides outside the web and maintains communication with the orb by means of a line attached to the center of the orb; the male climbs onto the web and jerks the female's communication line in a species-specific manner (Locket and Bristowe 1926).

Within level three Platnick positions visually acute spiders, such as the Salticidae (jumping spiders) and Lyssomanidae (ant mimics). An apogee of visual courtship is found in the mutual display of Lyssomanes bradyspilus. Courtship consists of retinal movements of the anterior median eyes. There is expansion and contraction of the black areas (retina) until the spiders make

contact and copulation proceeds from there (Platnick 1971).

The spider under investigation in this study, Mecyanogea lemniscata, is an orb-weaving spider (Araneidae) which constructs an extremely complex three dimensional dome-shaped orb web. Based on evidence from other species, M. lemniscata should display adaptation of sexual behavior particular to its unique web and should fit in level two of Platnick. This study investigated the sexual behavior of M. lemniscata with special reference to the modifications of its behavior relative to its unique web.

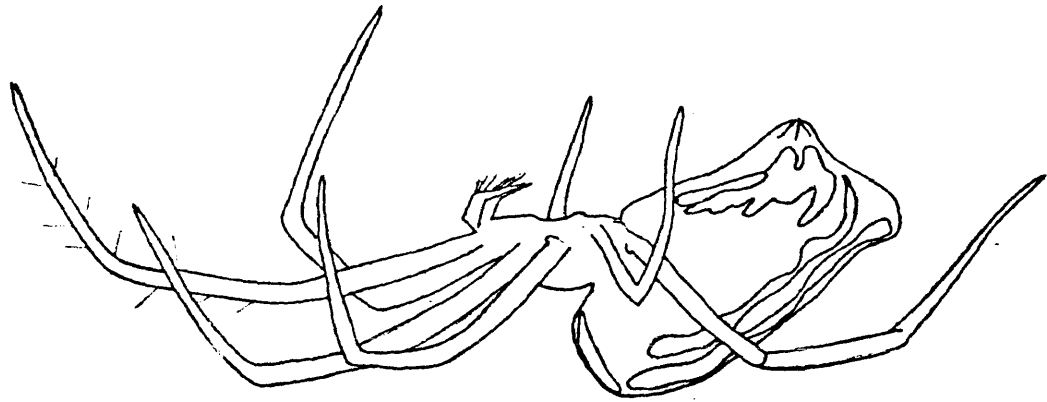
GENERAL DESCRIPTION OF MECYANOGEA LEMNISCATA

Mecyanogea lemniscata is an araniid (orb weaving) spider (figures 1 and 2) found in the southeastern United States (Levi 1968) and possibly as far south as the Canal Zone (Lubin, personal communication).

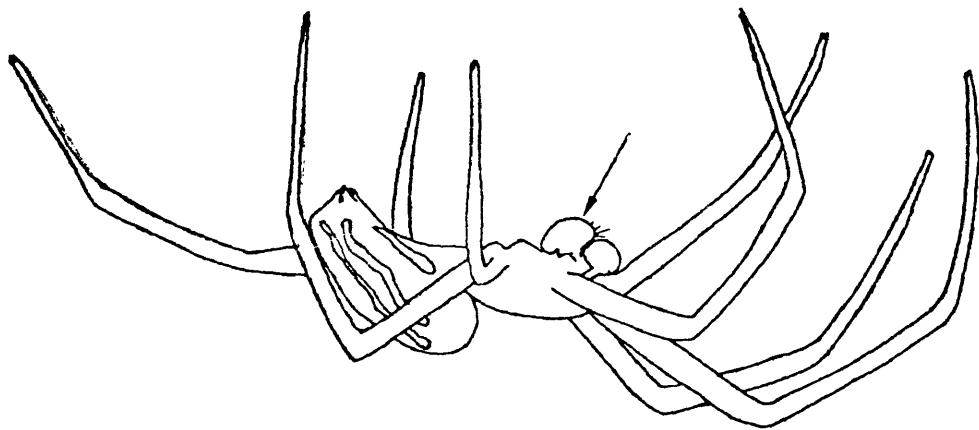
This species is an atypical araniid since it builds an unusual, horizontal, dome-shaped orb-web (figure 3 and table 1) which closely resembles the web of only one other araniid, the tropical spider genus Cyrtophora (Marples 1949 as cited by Blanke 1972, Kullman 1958, Lubin 1973). The dome portion of the web is a fine-meshed orb, and the mesh at the periphery is the same size as the mesh in the center. In a typical araniid orb the mesh in the center is smaller than that at the edge. M. lemniscata produces an even meshwork by placing secondary radii in the periphery of the orb as the spiral thread is placed. The dome is supported from above and below by a seemingly random matrix of threads which are attached to some stable structure such as the branches of holly (Ilex). The portion of the web under the dome is comparatively thread free, thus allowing the spider to move relatively unincumbered in this area. The web functions as a knockdown trap. Flying insects encounter the matrix threads above the dome and fall onto the dome. The orb is constructed of non-viscid (non-sticky) threads, which is also exceptional for an araniid spider. The fine mesh of the orb

Figure 1. Female Mecyanogea lemniscata

Figure 2. Male Mecyanogea lemniscata arrow indicates modified
pedipalp of the male



1



2

Figure 3. Web of Mecyanogea lemniscata horizontal dome shaped orb is suspended by a matrix of threads from above and below. Arrow at A shows where the dome is pulled down by an attachment from the lower matrix. Arrow at B points out attachment of the upper matrix to the mesh of the dome. Arrow at C shows lower attachment thread. Scale equals 10 cm.

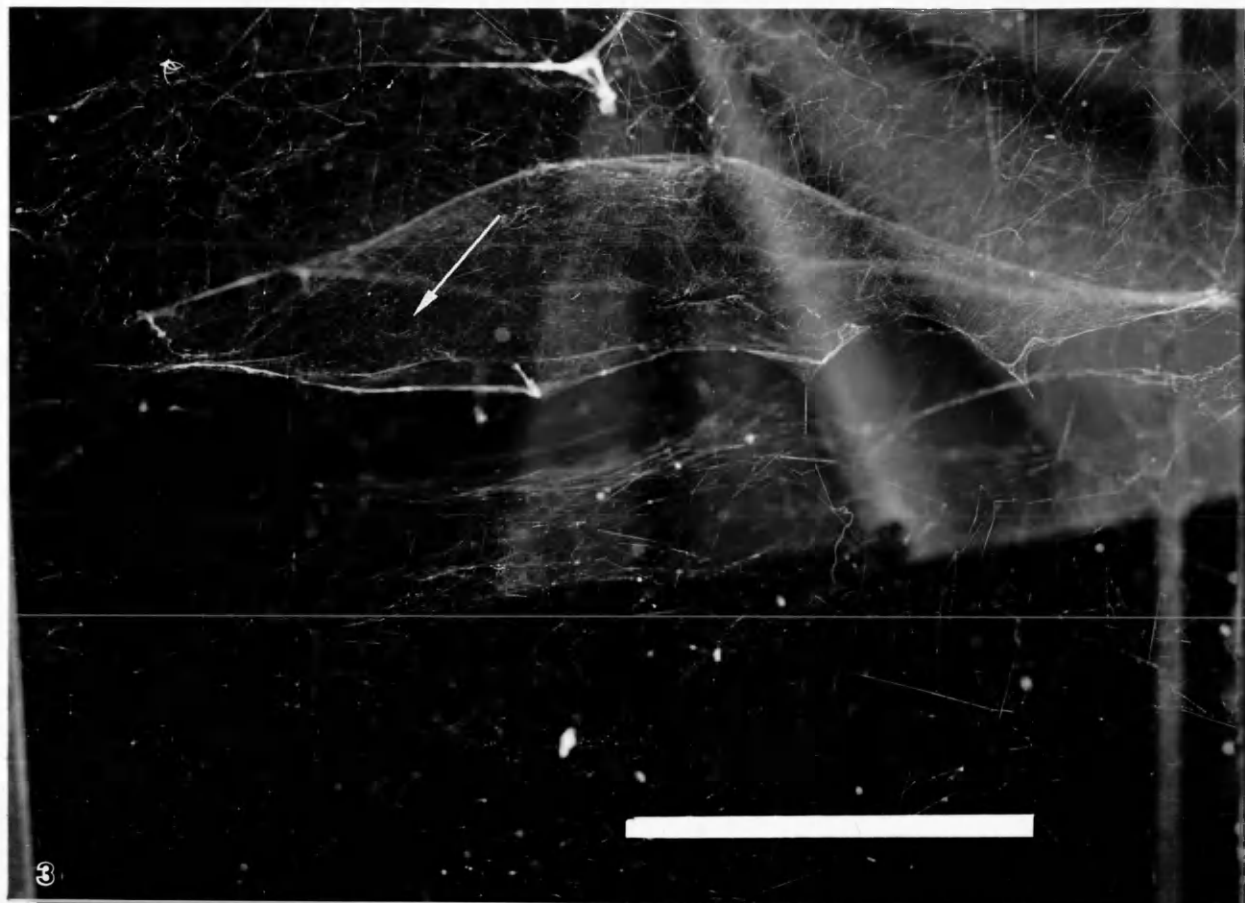


Table 1. Measurements of the three-dimensional web of
Mecyanogea lemniscata.

	RANGE*	MEAN \pm SD
Height	17.78-96.52	40.65 \pm 13.80
Length	20.32-68.58	43.50 \pm 11.64
Width	16.51-71.12	37.00 \pm 11.30
Diameter of Dome	9.53-27.94	19.72 \pm 4.74

*All measurements are in centimeters

Based on 68 webs

subrogates the viscid silk of other araneids, for insects are often seen caught in the meshwork of the orb by the hairs of their legs.

M. lemniscata has one generation per year in the Williamsburg area. Young emerge from the eggcases in May and mature through the summer months. Males mature approximately two weeks before the females, at which time they leave their webs and wander over the vegetation. Due to the reduced vagility of this species and to the fact that they sometimes construct colonial webs, a male has little trouble finding a female's web. The male will either live in the supporting matrix of an immature female's web until her final molt or roam until he finds the web of a mature female. Exline (1948) reported that the males of Allepeira lemniscata (Allepeira = Mecyanogea, Kaestner 1968) do not build orb webs; however, this is not true. Males of M. lemniscata have built complete species-specific orbs in the laboratory throughout this study, until their final molt.

The sexes exhibit reduced sexual dimorphism, with the male being darker in color with longer legs and only slightly smaller in size than the female. For many of the orb weavers this is not the case. In Meta segmenta (Blanke 1973b), Araneus curcurbitinus (Blanke 1973), Argiope sp. (Kaston 1948), and Cyrtophora citricola (Blanke 1972) the males are much smaller than the females.

METHODS AND MATERIALS

Field observations on sexual behavior were conducted during the summers of 1974, 1975 and 1976 in three different areas around Williamsburg, Virginia (holly vegetation adjacent to Crim Dell, Lake Matoka woods and in a wooded area behind Williamsburg East Apartments, Route 143).

Laboratory observations and filming of sexual behavior took place in 1975, 1976 and 1977. Plexiglas cages, 41.3 cm X 42.0 cm X 62.2 cm (figure 4) held spiders for observation during the early stages of laboratory study. The cages were equipped with special frames on which the spiders could spin their webs. The frames (figure 4) consisted of a square wooden base fitted with dowels of various lengths glued into the base at approximately 60° angles. While housed in these cages, the spiders were fed insects daily from sweep-net collections.

Later in the study, a 174 cm X 290 cm X 274.3 cm room (figure 5) was constructed in the basement of Millington Hall to house the spiders. The room, painted flat black inside to reduce glare for filming, was equipped with a Sears Automatic Console Humidifier and a bank of fluorescent lights. Temperature ranged from 18° to 30°C and the humidity was approximately 50 to 65%. A light cycle of sixteen hours light and eight hours dark was maintained.

Figure 4. Plexiglas cage with wooden frame

Plexiglas cage, black arrow shows screen in access port, screen is also present on floor and the far end panel. Wooden frame, white arrow points to a dowel used by the spider as support for its web.

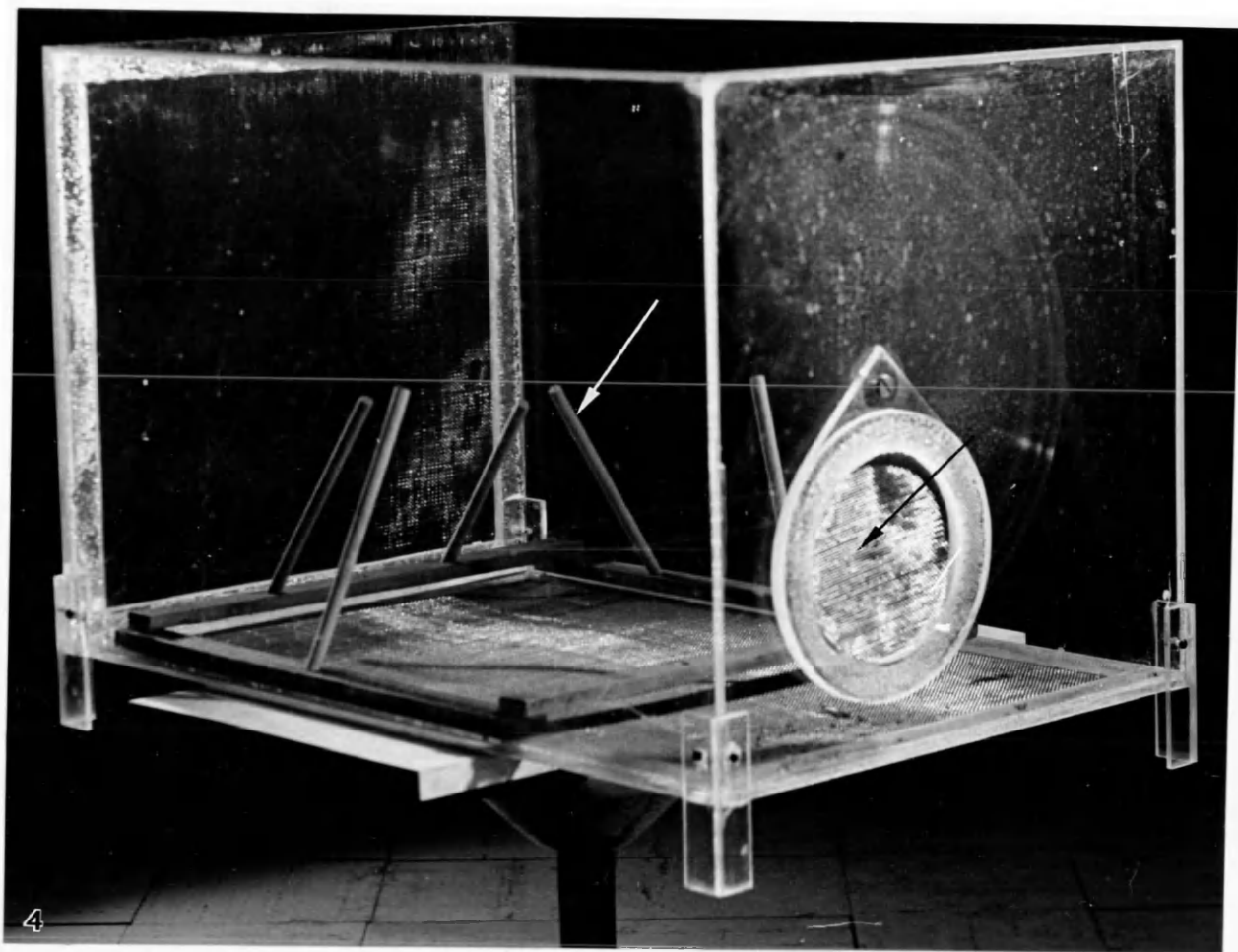
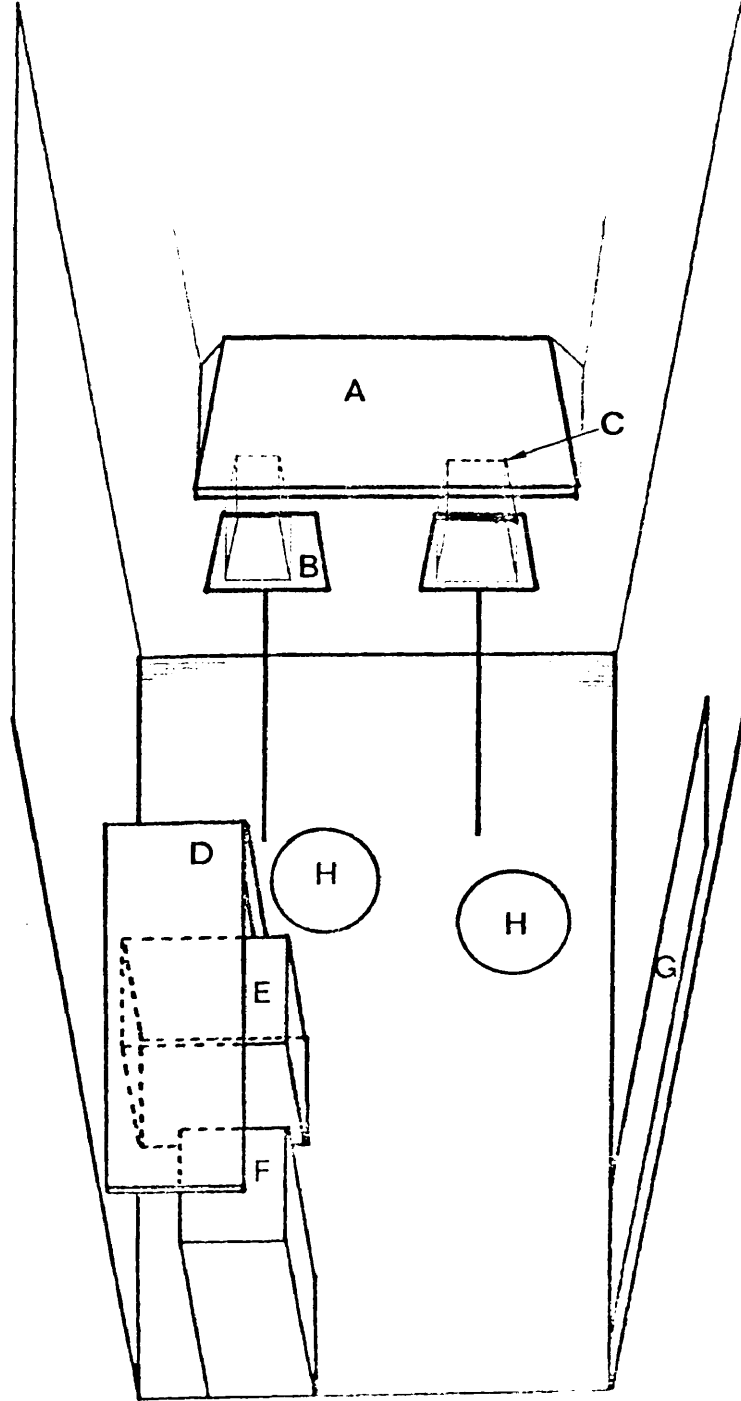


Figure 5. Spider room A is a bank of fluorescent lights, B platform for frames, C frame for spider to build web, D workbench, E Plexiglas cage, F humidifier, G door, H positions for camera.



Immature spiders were collected from the field for use in studying mating behavior. By taking advantage of their natural tendency to drop from the web when sufficiently alarmed, specimens were obtained by placing a jar beneath the web and shaking the vegetation. Eggcases were collected later in the season, and spiderlings from these eggcases were cultured to provide adults for laboratory study when the natural population was overwintering. The spiderlings were dissected from the eggcases and placed in "pseudoeggcases" (figure 6) to speed development. Pseudoeggcases consisted of jars one-half filled with water to maintain high humidity and fitted with gauze over the mouth to support a bed of cotton in which the spiderlings were placed. After two to four weeks the spiderlings were transferred to small wooden frames, 6.35 cm X 6.35 X 8.9 cm, upon which they spun webs (figure 7). Spiderlings were supplied free flying Drosophila melanogaster for food. Under these conditions they matured in approximately two to two-and-one-half months, with the males undergoing six to seven molts and the females seven to eight molts.

Spiders were isolated before fully mature by placing individuals in 11.4 cm X 10.2 cm X 23.5 cm plastic boxes covered with gauze. Each box was supplied with an open culture of D. melanogaster for food, and the gauze was moistened daily with a spray-mister. In this way all behavior to be performed would be observed when the sexes were put together for the first time. To study mating behavior, the females were placed on 25.4 cm X 25.4 cm X 25.4 cm or 30.5 cm X 30.5 cm X 30.5 cm wooden frames and allowed to build their webs.

Figure 6. "Pseudoeggcase" A jar half full of water, A.
indicates cotton bedding for the spiderlings,
B. points to rubber band holding the gauze over the mouth
of the jar.

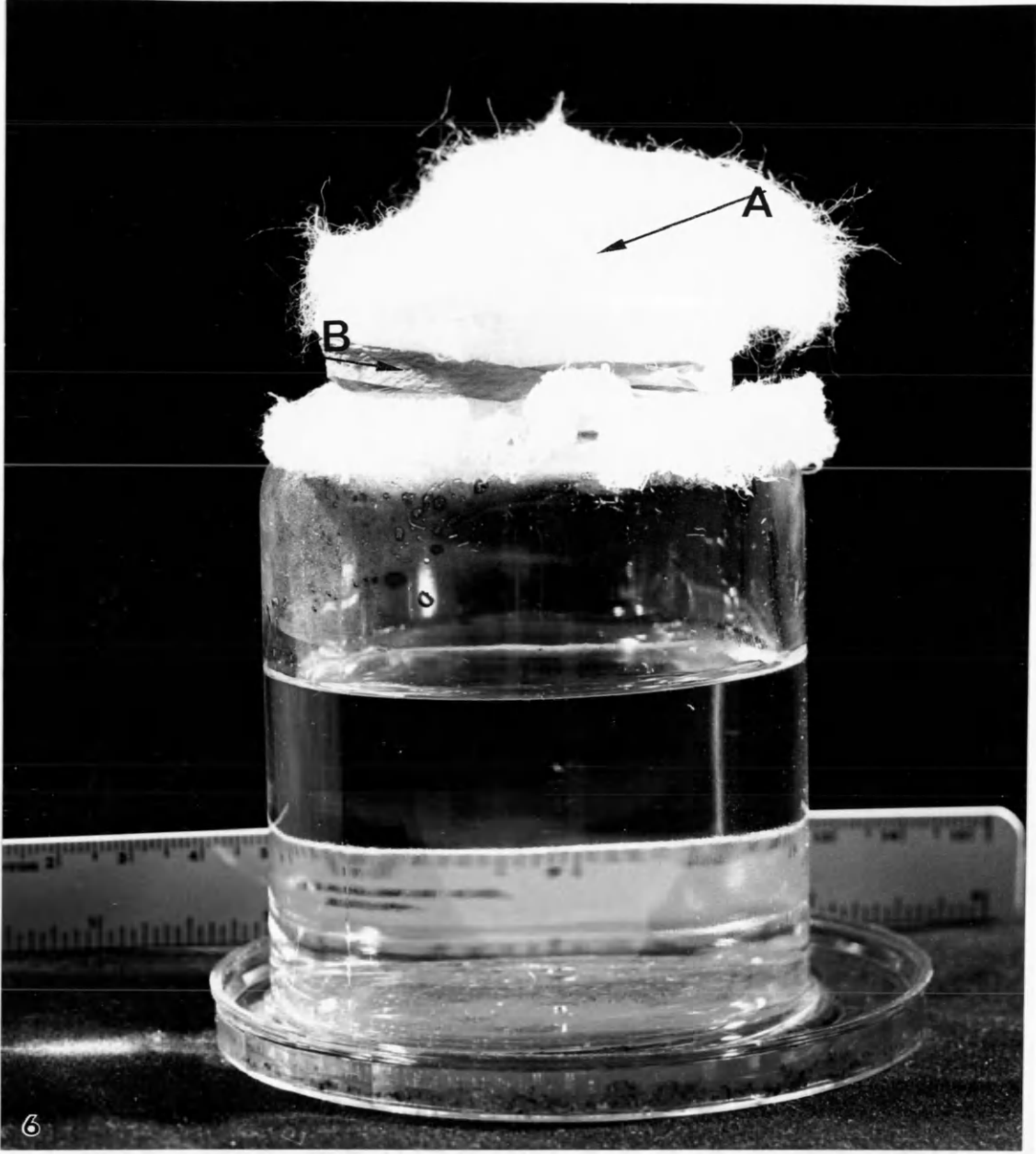
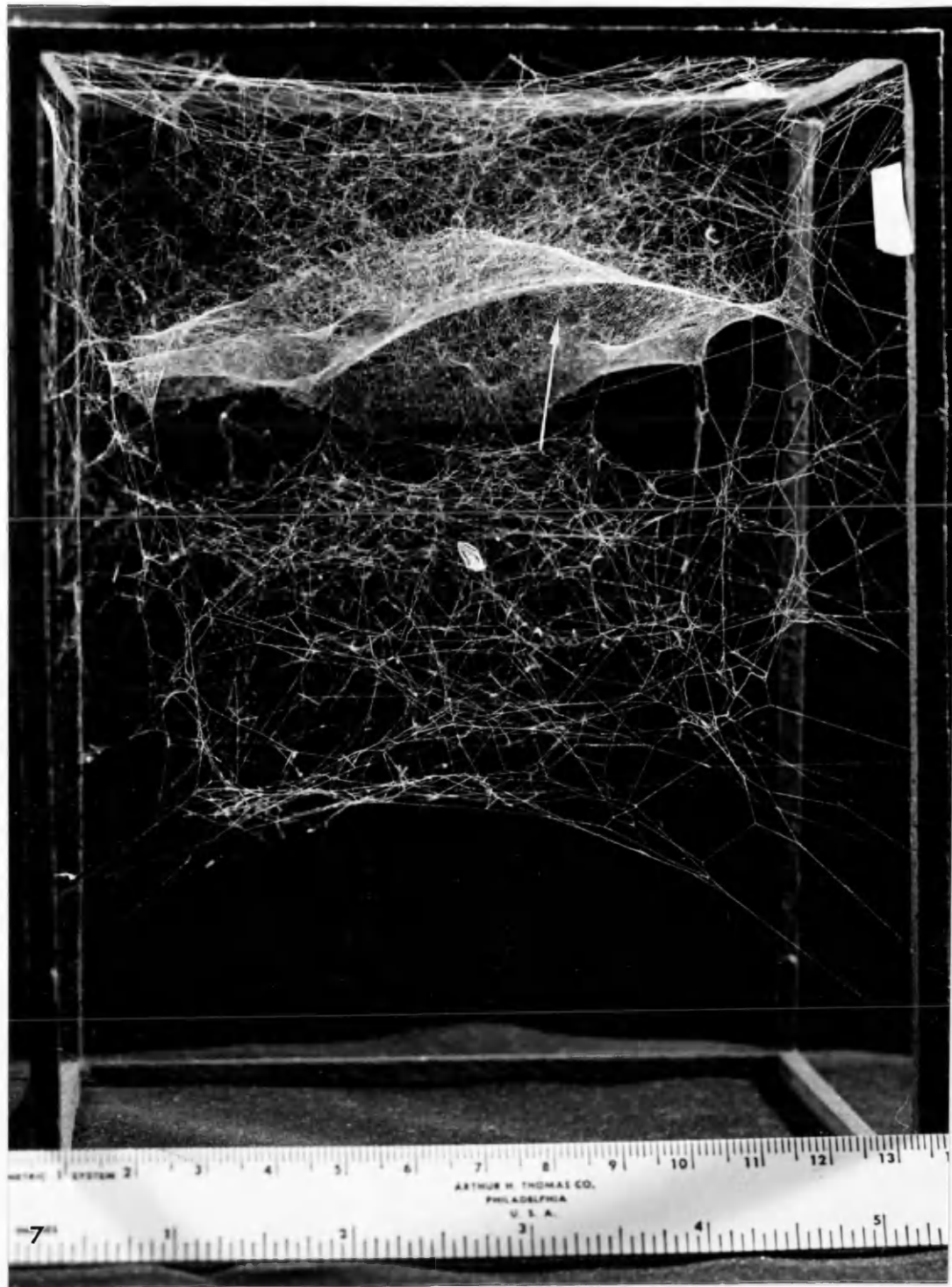


Figure 7. Web of immature M. lemniscata. White arrow shows mesh of the web. Note that all components of the immature web are the same as figure 3.

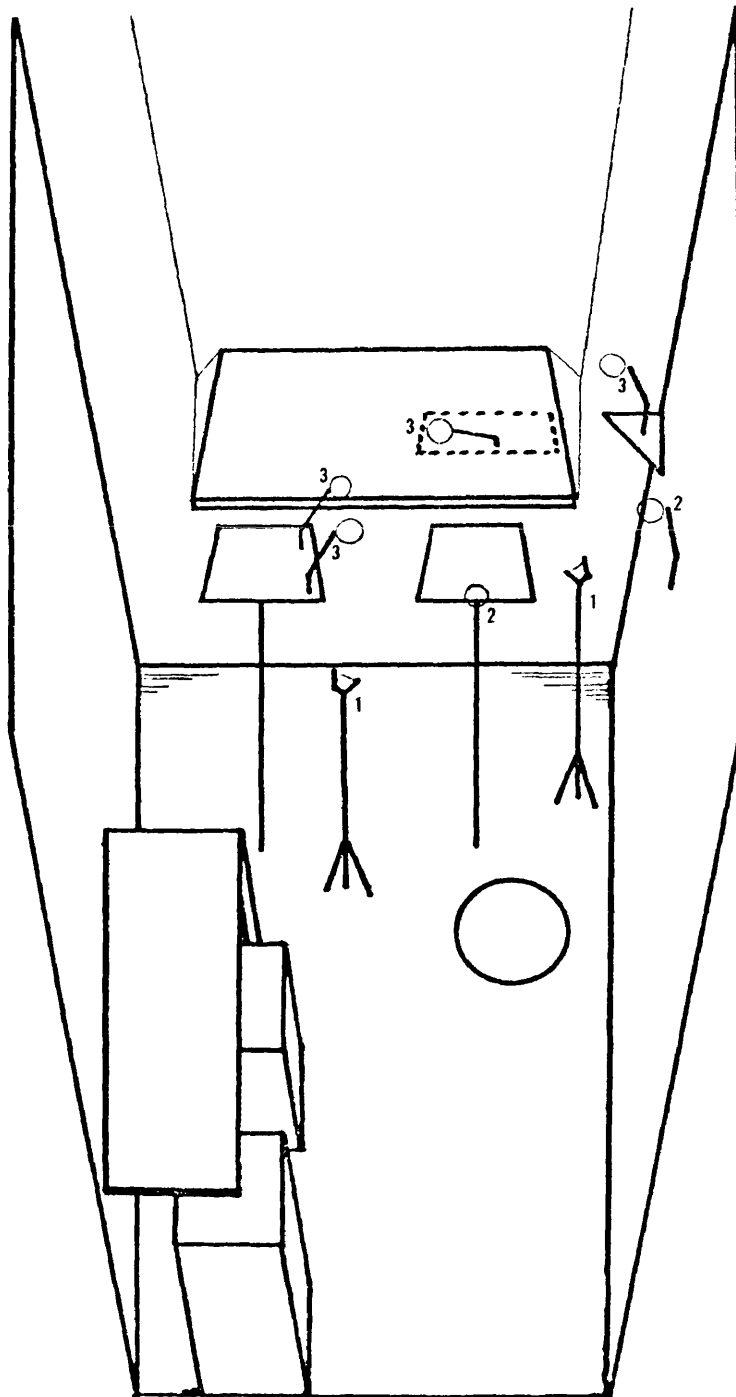


Mature males were then released onto the frames and mating behavior was noted or filmed.

Mating behavior was filmed at 24 frames per second using Ektachrome ER movie film (ASA 160) and a Bolex H-16, 16mm movie camera, equipped with an f/2/50 mm Kinoptik lens. Illumination for filming was provided by the regular bank of fluorescent lights as well as two Smith Victor floodlights, four hi-intensity study lamps and two 100-watt desk lamps (figure 8). A Sekonic Studio Deluxe Model L-28c2 light meter provided proper lens aperture and shutter settings. Films were analyzed on a variable speed 16 mm projector (equipped with a single frame feature) and a Craig Projecto-Editor film editor.

Photographs of the genitalia were taken on a Ziess photo-microscope. The male palpal organ by expanded before photographing by the method of Shear (1967). Artificial expansion of the palpal organ makes it similar in appearance to the expanded palpal organ in a copulating male.

Figure 8. Lighting arrangement, 1 indicates a Smith Victor floodlight, 2 indicates a 100-watt desk lamp, 3 denotes a hi-intensity study lamp.



RESULTS AND DISCUSSION

I. SPERM INDUCTION

Fertilization in spiders curiously entails two separate processes on the part of the male: sperm induction and sperm transfer. Sperm induction is the process whereby the palpal organ is filled with sperm, and sperm transfer is known as copulation.

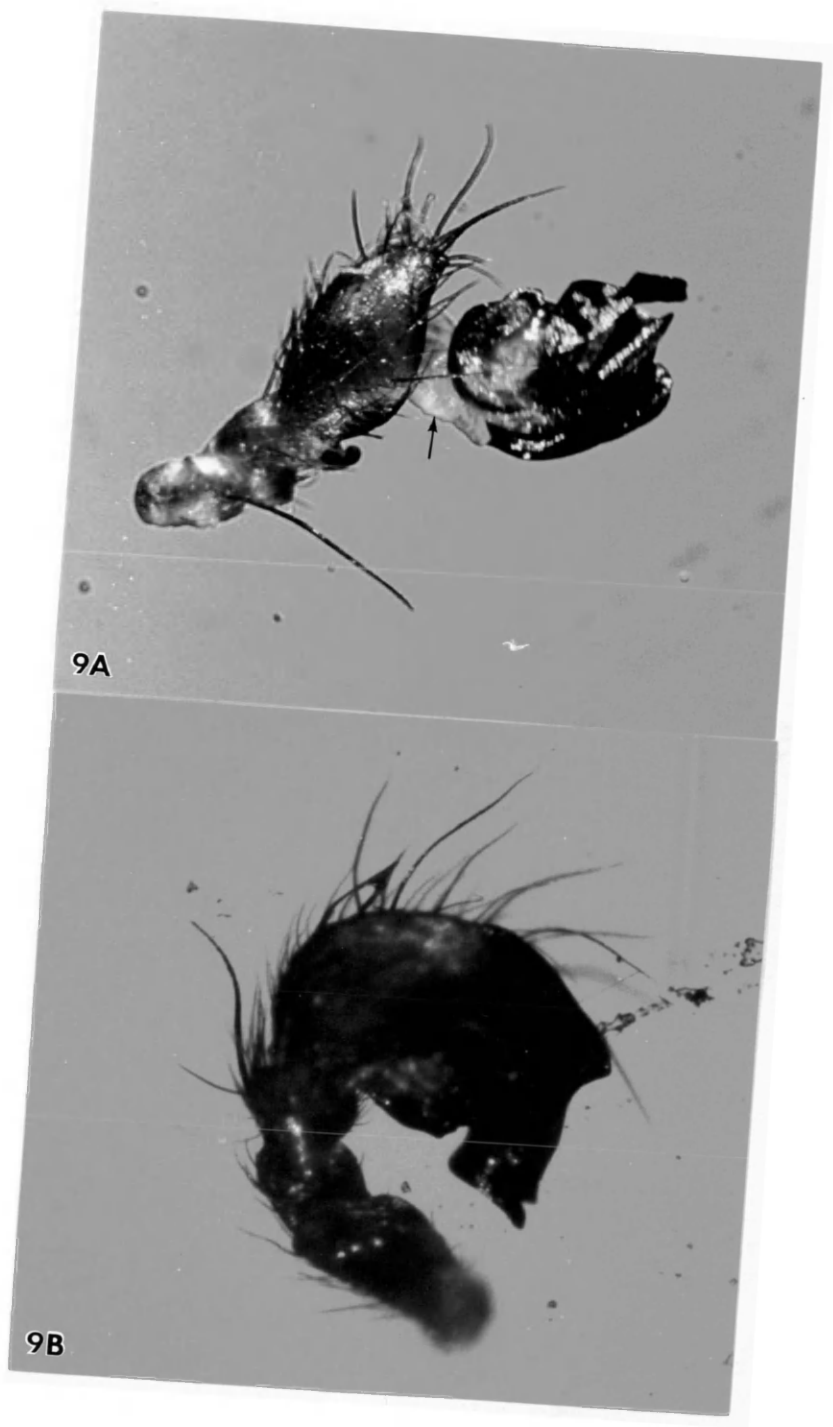
Alexander and Ewer (1957) address the question of how this double process came into being. It is suggested that the proto-spider transferred sperm by placing a spermatophore on the substrate, as in scorpions (Angerman 1955, Alexander 1956, and Zolessi 1956 as cited by Alexander and Ewer 1957) and some pseudo-scorpions (Kerr 1912 and Vachon 1938 as cited by Alexander and Ewer 1957) of today. The pedipalps may have served to either transfer spermatophores or to hold open the genital orifice of the female as she picked up the spermatophore. It is further suggested by Alexander and Ewer that the evolution of web-building coincided with the loss of the spermatophore, and the retention of palpal involvement in sperm transfer. This resulted in the evolution of the specialized organ of the pedipalp used by all contemporary spiders (figure 9).

Sperm induction was first described by Menge in 1843. It is accomplished by the male spinning a small sperm web upon which he deposits a drop of seminal fluid (Rovner 1966). The palpi are applied to the drop in order to charge the palpal organs. Cooke

Figure 9. Male palpal organ of Mecyanogea lemniscata.

Figure 9A. Expanded palpal organ. Arrow points to the expanded hematodocha.

Figure 9B. Unexpanded palpal organ. Arrow points to chitinized portions of the palp.



9A

9B

(1965) suggests that the sperm is drawn into a duct in the organ by the possible resorption of a fluid previously secreted by surrounding glands.

The palpi are applied differently to the drop of seminal fluid in different species. The majority of spiders apply the palpi in an alternating fashion from the same side of the web from which the drop was placed. Such behavior is seen in Lycosa rabida (wolf spider) (Rovner 1966) Cyrtophora citricola (Blanke 1972) and in the species under study in this paper, Mecyanogea lemniscata. In the genus Dysdera the male reaches underneath the sperm web and inserts both palpi simultaneously into the drop (Cooke 1965). Linyphia triangularis (sheetweb weaver) releases the drop onto the sperm web and then assumes an inverted position under the drop. He charges his palpi by drawing the seminal fluid through the web (Rovner 1967).

Sperm induction has not been observed in M. lemniscata without the presence of a mature female. Bristowe and Locket (1926) found that some spiders perform sperm induction only in the presence of a female, and this seems also to be the case for M. lemniscata.

Sperm induction has been observed in M. lemniscata after copulation. Until recently it was believed that male spiders would not display courtship unless they had proprioceptive feedback which indicated that the palpal organs were full, (Gerhart 1924 as cited in Rovner 1966, Kaston 1948, and Gering 1953 as cited in Rovner 1966). Rovner (1966) forced subadult males of Lycosa rabida to amputate their palpi by tying the tibiotarsal joint of both palps to one side of a cage while the spiders were under carbon dioxide anesthesia.

When the males recovered they pulled off their palpi by moving away from the wall. Thus in the adult stage these males lacked pedipalps. The males went through the motions of sperm induction, courtship, and copulation with a female. The data indicated to Rovner that control of sperm induction, courtship and certain aspects of copulation is central. Blanke (1971) also found that a male Cyrtophora went through the normal motions of sperm induction with one palp missing. Therefore, male spiders do not need charged palpal organs to court, and some may only charge their palpal organs in the presence of a female. The males of M. lemniscata often do not perform sperm induction until they have gained entry into a female's dome or until after the first copulation. This behavior would certainly insure viable sperm for copulation; however, it is not known how long sperm does remain viable in the palpal organ.

The following account of sperm induction by a male M. lemniscata is taken from laboratory observations. The male first climbs out of the female's dome and walks about the supporting matrix. He then situates himself in an area off-center to the hub of the dome and clears the area by biting away the female's matrix threads. The cleared area is not large - approximately two centimeters in diameter and roughly spherical. In this area he places a few threads at an angle by starting distal to the hub and moving proximally. As each thread is placed, the male plucks on it in a manner very similar to peripheral dome strumming in introductory courtship behavior except that the frequency is much slower, as in matrix plucking. This plucking probably identifies the male to the female and thus prevents

her from attacking during this crucial behavioral sequence. The plucking rhythm is relatively slow, (table 2, figure 10) and accomplished primarily as in other thread vibrating sequences by the third pair of legs.

After placing ten to fourteen threads in the above manner, the male places two final threads which are longer than the others and forms a narrow inverted "V" (figure 11). The male hangs inverted from these threads with his fourth legs towards the angle of the "V". He positions his spinnerets three-fourths of the way up the "V" and then fills in the area between the threads with silk. The resulting mat is approximately 1 mm X 2 mm. The spider next aligns his epigastic furrow (figure 12) with the mat and with a series of ten to twenty rhythmic movements ejaculates a small drop of seminal fluid onto the mat. He quickly moves to bring his pedipalps into position with the mat and applies them to the drop. The palps are first applied in quick alternation, less than one second per palp. The pace is gradually diminished until the process ends with the palpi applied for approximately twenty seconds each. The entire process takes from eight to ten minutes. Blanke (1972) found that Cyrtophora citricola also demonstrated a similar timing sequence for palpal application.

After sperm induction the male moves from the sperm web to the matrix where he intensively cleans his pedipalps and legs, after which he may either return to the dome and continue mating or remain in the matrix.

Figure 10. Thread plucking during sperm induction.

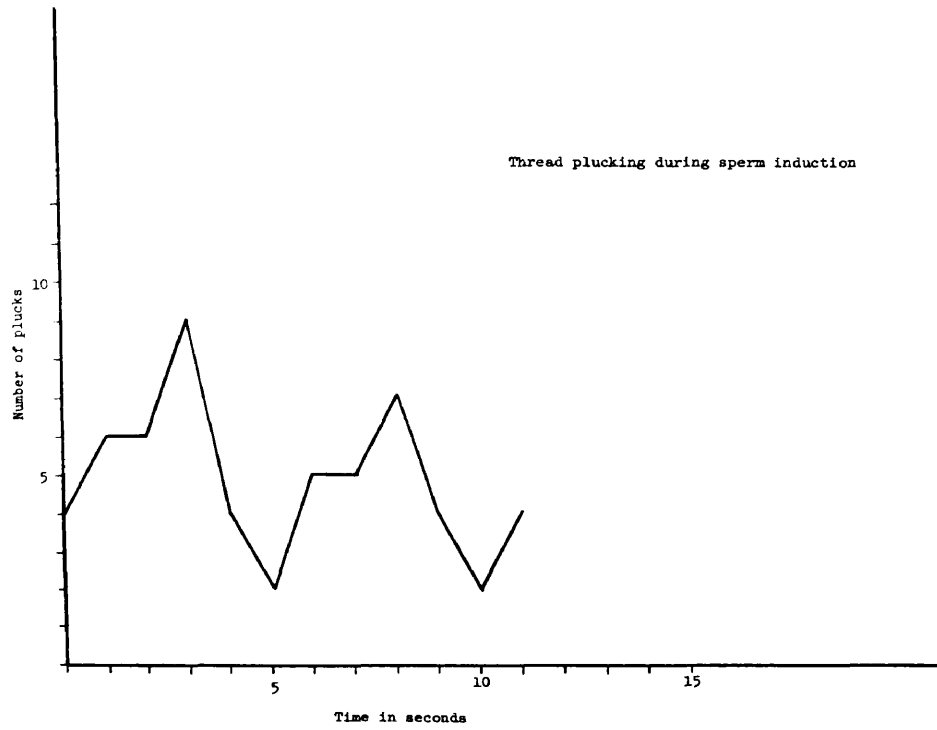


Figure 11. Schematic web of Mecyanogea lemniscata. A. points to the sperm web of the male, B. is the nuptial thread, C. denotes the lower matrix of the web.

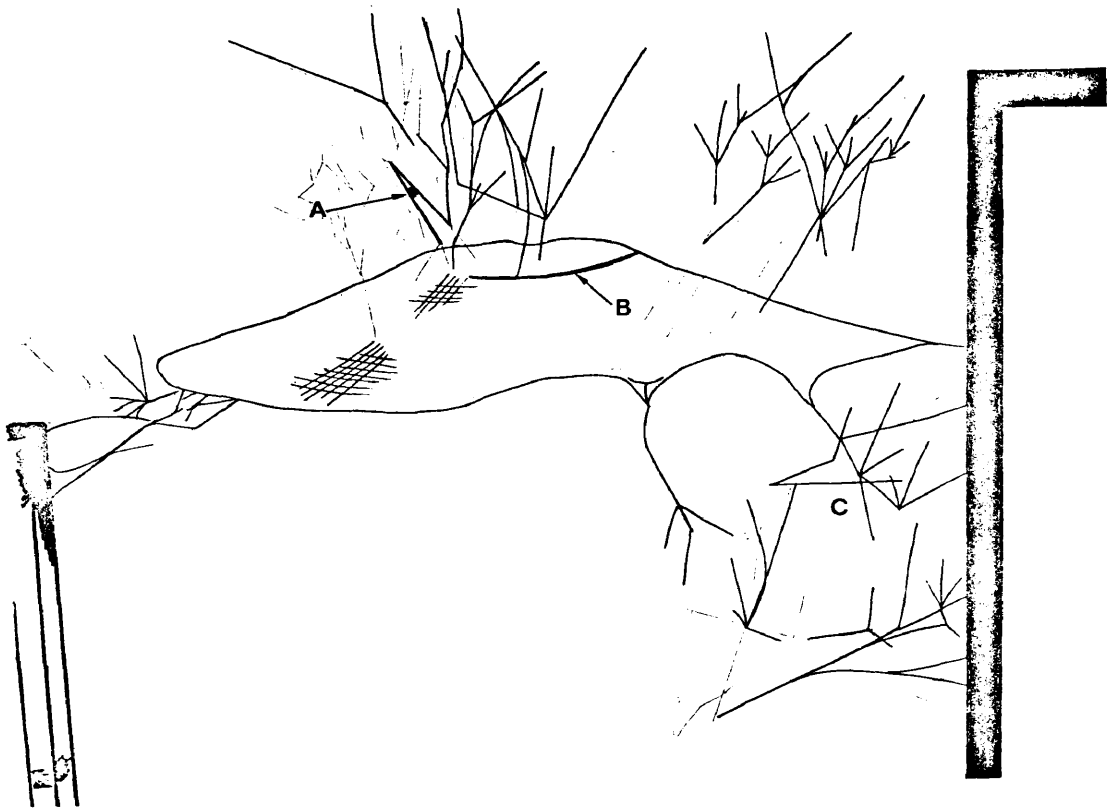


Figure 12. Epigastric furrow of the male.



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II. COURTSHIP

Courtship in orb weaving spiders has been reported by Montgomery (1908), Locket and Bristowe (1926), Saito (1931 as cited in Platnick 1971), Kullmann (1964), Mascord (1966), and Blanke (1971, 1973, 1974b). The male display is quite conspicuous and has been subjected to natural selection (Platnick 1971). The evolution of courtship has resulted in species-specific behavioral sequences in spiders. Within the orb weavers there have developed differences which may have served to increase the success of the particular species. An example of this is reported by Blanke (1974). Meta segmenta males make use of the female's predatory behavior for mating purposes. The male waits for a female to capture prey, and then drives her away from her meal. The female returns to the prey to find a courting male. Courtship ensues and copulation is the end result. Blanke (1973) also reports that in Araneus curcurbitinus the female holds the nuptial thread with her third pair of legs and thereby changes the angle of the nuptial thread relative to her epigynum. This allows the much smaller male to insert his palpal organs on the first attempt.

Mecyanogae lemniscata also possesses courtship behavior specific to its morphology and web structure. The courtship can be broken down into two stages: introductory courtship and epithalamic courtship. Introductory courtship is found in the literature but has never been distinguished from other parts of courtship. The physical and behavioral characteristics of M. lemniscata more clearly delineate the disjunction in courtship behavior, thus making the separation of the two stages of courtship behavior

necessary. The function of introductory courtship is to identify the male and facilitate his entry into the dome portion of the female's web.

Epithalamic courtship of M. lemniscata is actually a modified combination of Blanke's (1973) long and short distance courtship found in Araneus curcurbitinus. According to Blanke, long distance courtship begins with the male placing a nuptual thread in the female's web. Short distance courtship begins when the female assumes the copulatory or "ring" position (third legs pulling on the nuptual thread) and the male touches her mouth and sternal areas. Combining long and short distance courtship in M. lemniscata is justified, since this species may cohabit for an extended period of time during which mating may occur repeatedly. Once the male is accepted into the dome, a complex combination of reaction chains is exhibited which links the two courtship behaviors (long and short distance). Therefore in M. lemniscata Blanke's definitions are cumbersome and a more general classification is needed. For this reason the term "epithalamic" (Greek: epi = upon, thalmus = bed chamber) is applied to that portion of courtship behavior of M. lemniscata from the time the male places the nuptual thread until copulation.

A. Introductory Courtship

Introductory courtship of M. lemniscata is comprised of three types: 1) Matrix plucking, 2) Peripheral dome strumming, 3) and Charging.

Matrix plucking is performed by the male in the supporting matrix of the female's web. The male places one or two threads in

the matrix and suspends himself in an inverted position from them. He performs relatively slow plucking movements with his legs, averaging less than one pluck per second. Table three and the accompanying graph of matrix plucking (figure 13) demonstrates a general pattern of oscillation in the amplitude of plucking frequency. This general pattern is seen in all behavior sequences in which M. lemniscata uses thread plucking for communication. As discussed earlier, this same general plucking is seen during the construction of the sperm web. Such plucking behavior probably identifies the male and therefore prevents the female from leaving the dome and attacking him.

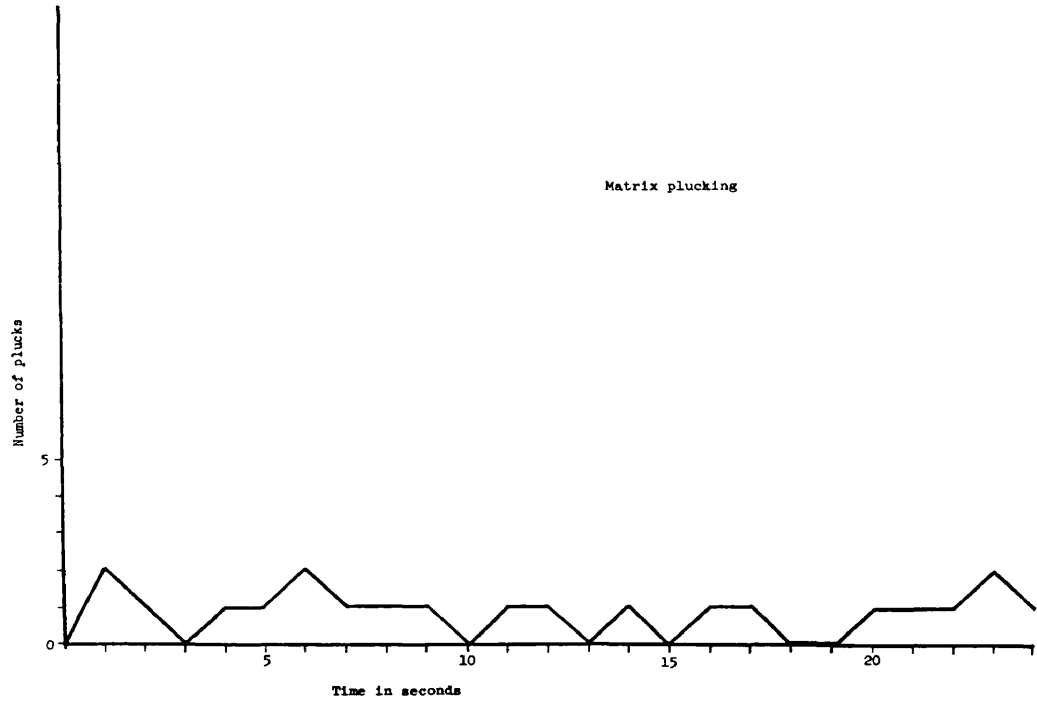
Matrix plucking by M. lemniscata is similar to the first encounter of female webs by males of other orb weaving species in that it is performed from a distance. Epeira curcurbitina, as reported by Locket and Bristowe (1926), spins some threads above the female's orb and starts a series of "jerking movements". T. H. Montgomery, Jr. (1908) stated that the male of Epeira mormorea begins at the outer edge of one radius and signals to the female by "tugs" on the line. The families of Araneidae and Tetragnathiae were referred to by Platnick (1971, p. 42) in the following manner: "An orb-weaving male remains on the outskirts of the female's web, tweaks threads with the forelegs, slowly approaches the female, builds a series of 'mating' threads onto the web, and tweaks these threads until the female is coaxed onto them for mating."

Table 3. Analysis of leg movements during matrix plucking.

Legs	RIGHT SIDE				Legs	LEFT SIDE			
	I	II	III	IV		I	II	III	IV
*									
				IV				III	
								III	
				IV					
		II							
		II		IV					
		II							
		II							
		II							
		II							
		II							
		II							
				IV					
				IV					
				IV					
								III	
				IV					
			III						
				IV				III	
				IV					
								III	
	I								
	I								
	I								

*Each space represents one second

Figure 13. Matrix plucking.



Once the male M. lemniscata has performed matrix plucking, he may move toward the dome and enter or simply remain at the edge of the dome and perform peripheral dome strumming, the second type of introductory courtship.

I have found nothing in the literature which resembles peripheral dome strumming behavior. It might be an adaptation to the combination of web structure and size of the male. The web structure (figure 3) is very complex and movement in the matrix portion of the web is slowed a great deal by the arrangement of threads. The relatively large male climbing through the matrix toward the dome can create vibrations which could evoke or re-evoke an attack by the female. Peripheral dome strumming may therefore act as a "booster", to re-identify the male and thus facilitate the mating process.

The actual strumming behavior (table 4 and figure 14) is rapidly performed with a general oscillation of amplitude as seen in other thread plucking behaviors. This, to a large extent, resembles nuptial thread strumming of epithalamic courtship. It should be pointed out at this time that the use of the word "pluck" in this study refers to thread vibrating behavior performed by the male in which he slowly uses one leg after the other on the thread. This is in contrast to the word strum, in which the male rapidly vibrates the thread(s) by often using more than one leg at a time.

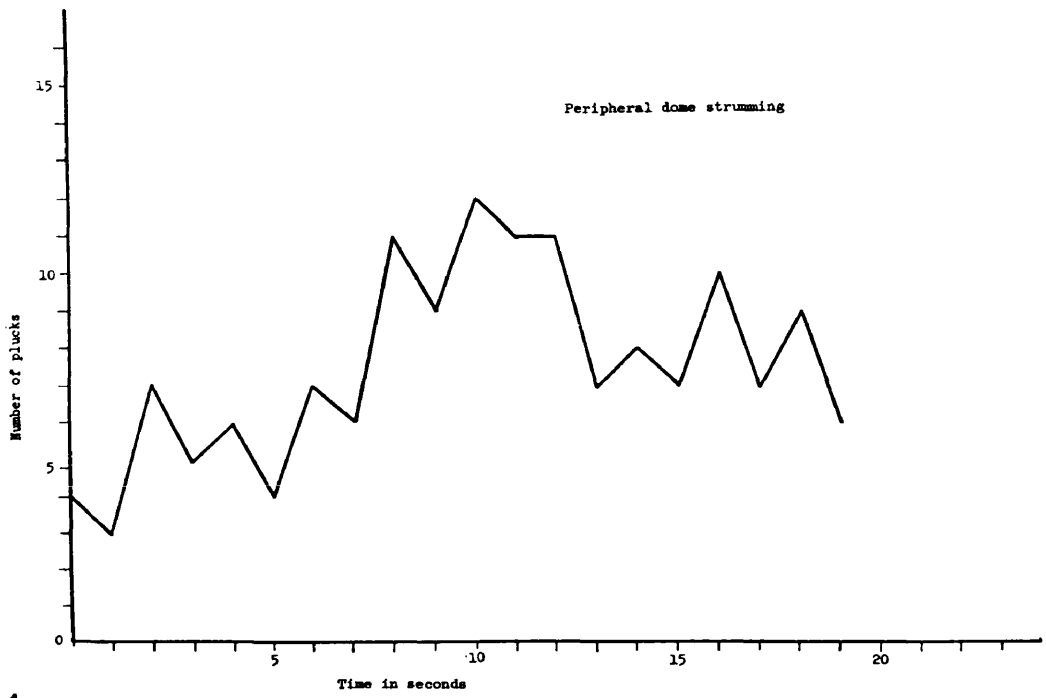
The third type of introductory courtship, charging, might best be described as a lack of introduction. The male performing this type of introductory courtship performs neither matrix plucking nor peripheral dome strumming. He simply walks or runs directly into the

Table 4. Analysis of leg movements during peripheral dome strumming.

Legs	RIGHT SIDE				Legs	LEFT SIDE			
	I	II	III	IV		I	II	III	IV
*		II	III						
				IV				III	
		II		IV				III	
	I			IV					
		II		IV					
			III		I				
		II						III	
			III					III	
				IV					
	I			IV					
		II							
			III					III	
				IV					IV
		II				II			
				IV					IV
		II							
	I			IV				III	
					I				
								III	IV
	I							III	
		II		IV		I			
			III						
	I		III		I				IV
			III		I			III	IV
	I			IV					
								III	

*Each space represents one second

Figure 14. Peripheral dome strumming



dome without identification. An approach by charging is very rare in spiders. Locket and Bristowe (1926) report that the male of Dictyna latens moves directly up to the female, maneuvers underneath her and applies his palpi. There is no previous identification of the male or courtship involved. M. lemniscata, however, does engage in courtship display, and charging is simply one method used to gain entry to the dome before performing epithalamic courtship.

A charging male always elicits a female attack. An attack may consist of merely leg wrestling at one extreme to the female driving the male away at the other. In any case, a male that exhibits charging behavior has never been observed to change his approach to one of the other introductory courtship behaviors, he continues to charge the dome until accepted by the female or completely rejected.

The fact that charging is a viable method of entry into the female's dome reflects the relative tolerance of some females. This tolerance, also shared by some males, is a prerequisite for the semi-colonial lifestyle of the species and the cohabitation of the sexes during the mating season.

B. Epithalamic Courtship

Epithalamic courtship is common to all orb weaving spiders. Simply stated, the male places a nuptial thread on the female's web and strums it. There is then a chain of courtship displays between the male and female which ends in copulation.

The epithalamic phase of courtship in M. lemniscata is frequently preceded by the male cleaning his pedipalps and legs. This activity

seems to be widespread among spiders. Blanke (1972, 1973) found that Cyrtophora citricola and Araneus curcurbitinus both engaged in similar cleaning activities. Locket and Bristowe (1926, p. 1134) state "This passing of the palps by the male through the chelicerae occurs during mating in all spiders I have watched." The assumed function is to arrange and lubricate the palpal organ before copulation.

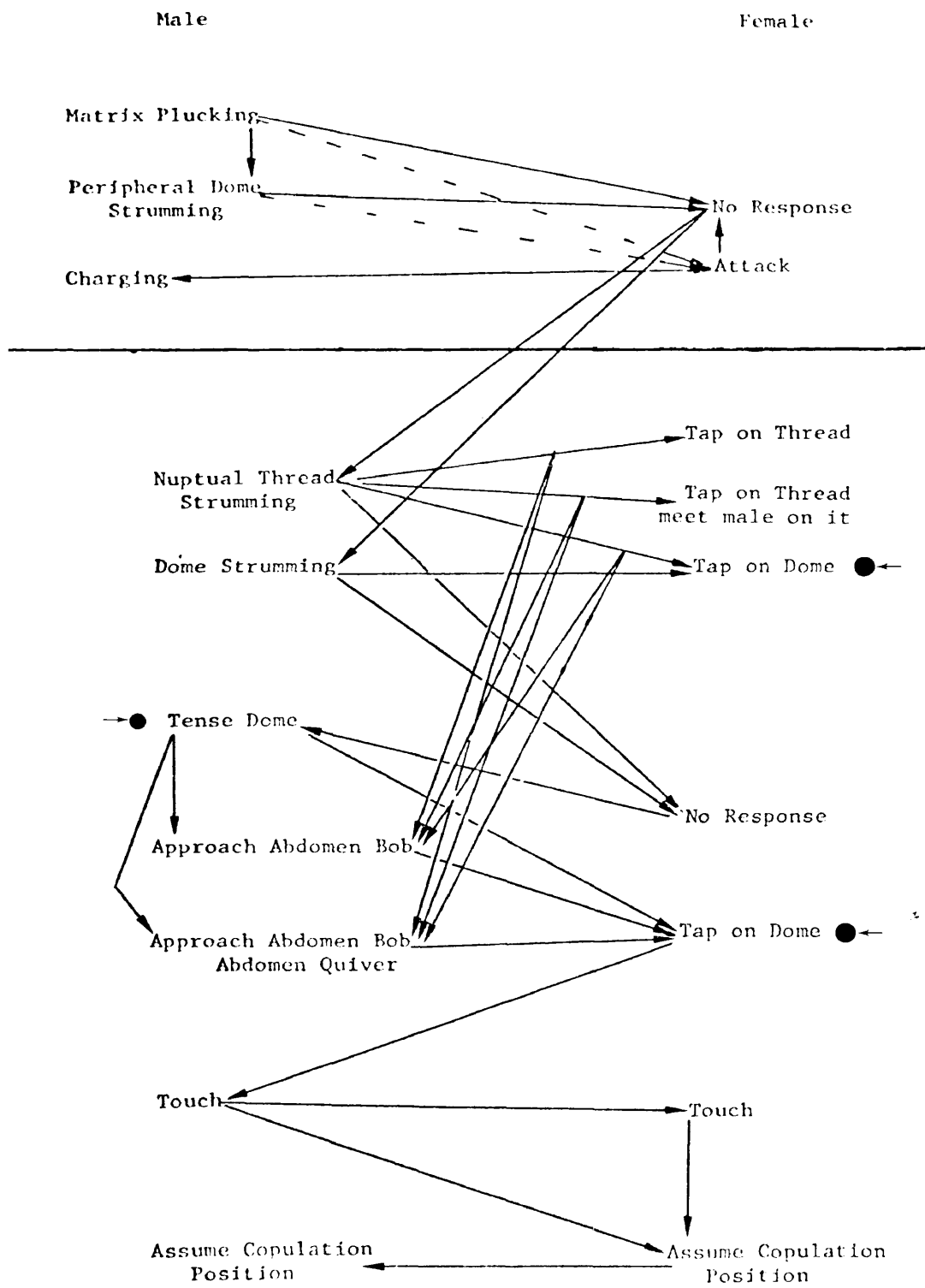
In his paper on the evolution of courtship behavior of spiders, Platnick (1971) extends Tinbergen's theory of vertebrate courtship as a releaser system to spiders, however Locket and Bristowe had forwarded this very idea in 1926. While speaking of Linyphia leprosa they state: "Her whole attitude is, in fact, one of complete readiness and eagerness for mating. Consequently the male's tactile display, although necessary (since the male must be recognized as such, least he be attacked), is much diminished, and has only a kind of trigger action on the female, whose movements now not only guide the male to her, but stimulate him in turn" (p. 1142, op. cit.).

The courtship of M. lemniscata is also a releaser system, and as figure 15 shows, the releaser system is intricate. This complexity in courtship reflects the complex life style of the species. The releaser system is composed of steps, each step leading to the next. Within these steps there exists a latitude of response, and this latitude of response is at first perplexing when judged against the belief that one step of the releaser system must provoke the next specific step if the chain is to continue. Such variation is not noted in other species. In Araneus curcurbitinus

Figure 15. Courtship releaser system of Mecyanogea lemniscata.

Behavior above the solid line is introductory courtship, that below the line is epithalamic courtship.

→● denotes the most likely position where an abbreviated reaction chain is initiated.



the female comes to meet the male on the nuptual thread once he has strummed upon it (Blanke 1973). It is necessary in this species for the female to perform this specific behavior if mating is to continue.

The epithalamic courtship releaser system of M. lemniscata begins when the male places a nuptual thread (figure 10) across a portion of the female's dome, in most cases near the center, and strums on it (figures 16 and 17). The releaser system may also begin when a male performs strumming directly on the dome. Both variations of this initial step have been observed to be performed by the same male. Table 5 shows an analysis of leg movements of nuptual thread strumming. The same general pattern of oscillating amplitude of plucking frequency is seen. Blanke (1972) reports for Cyrtophora citricola that the plucking frequency of the male upon the nuptual thread gradually ascends from ten strokes per second to eighteen strokes per second. M. lemniscata displays a strumming frequency in the same range, using from six to seventeen strokes per second.

The female signals to the male in one of three ways. She may a) tap on the nuptual thread, b) tap on the nuptual thread and meet him on it or c) tap on the dome. The female must perform this tap at some time during epithalamic courtship if copulation is to proceed, although the fact that the tap is performed does not guarantee that copulation will follow. Hans Lind (1976, p. 163) pointed out: "In apparently externally regulated chain

Figure 16. Nuptual thread strumming of Mecyanogea lemniscata.

The interval separating the positions in frames A, B and C is $1/24$ of a second. Note that legs 1 and 2 each pluck the thread one time during the time of the three consecutive frames. Drawn from a film of nuptual thread strumming.

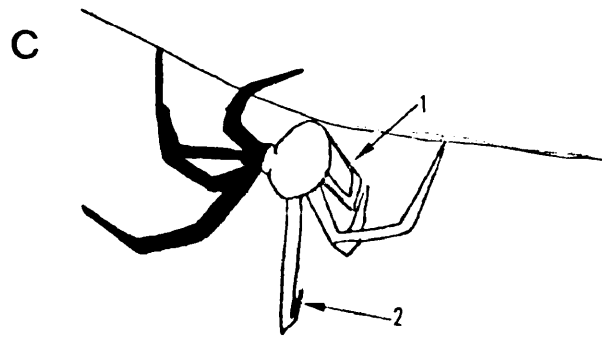
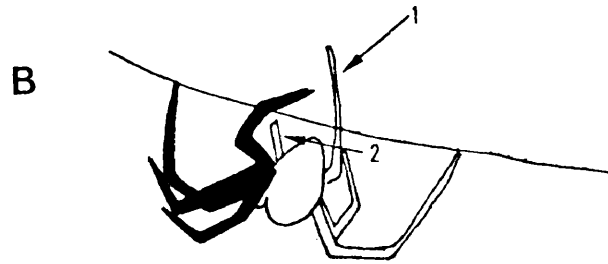
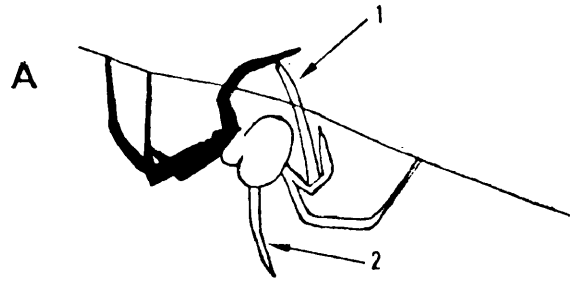


Figure 17. Graph of nuptual thread strumming of Mecyanogea
lemniscata. Nuptual thread strumming is rapidly per-
formed with a large amplitude (plucks per second)
and a high frequency (rapid change in amplitude).

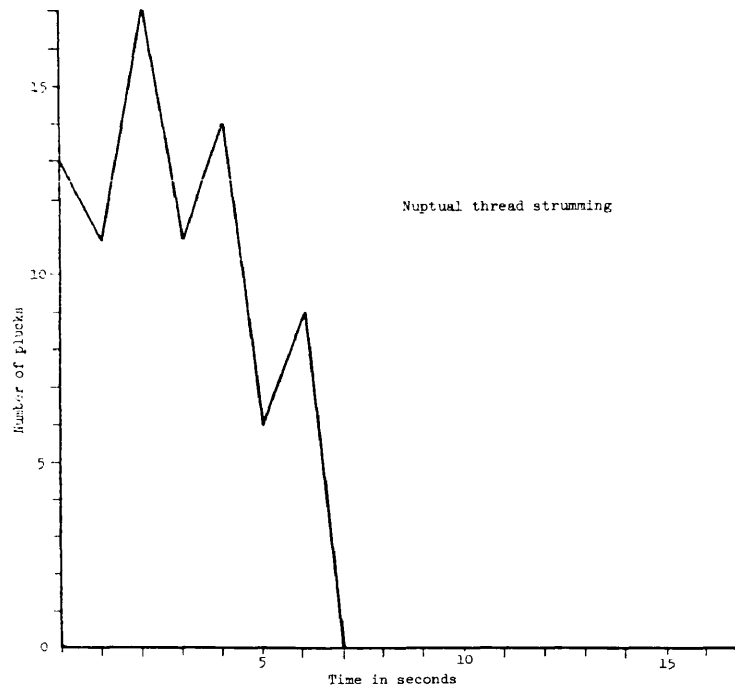


Table 5. Analysis of leg movements during nuptial strumming.

Legs	RIGHT SIDE				Legs	LEFT SIDE			
	I	II	III	IV		I	II	III	IV
		II	III°			II	III°		
			III°				III°		
			III°				III°		
			III°				III°		
						II			
			III°				III°		
			III°				III°		
			III°				III°		
			III°			II			
			III°				III°		
			III°				III°		
			III°				III°		
		II					III°		
			III°				III°		
			III°				III°		
			III°				III°		
			III°				III°		
			III°				III°		
		II				II			
			III°				III°		
		II					III°		
			III°				III°		
		II				II			
			III°				III°		
			III°				III°		
			III°				III°		
		II				II			
			III°				III°		
			III°				III°		

*Each space represents one second

°Indicates that two legs were used simultaneously

responses the role of the external stimuli may be permissive rather than decisive." Therefore M. lemniscata has a choice, the female taps either on the nuptual thread or the dome itself, for both meet the criteria of being able to transmit vibrations. Therefore it is not surprising that courtship behavior does continue when either response is given.

In the event that the female does not tap in response to the male's strumming, the male will leave the nuptual thread (if he was on it) and take hold of the dome with all eight legs and tense the dome by contracting his legs. This behavior of tensing the dome is also seen in prey capture. It is assumed that an object on the dome, whether prey or the female, will vibrate after the dome has been tensed and thus reveal its position. The male may then approach the female with a series of "strides". If the female does respond to the male's strumming with a tap, the male approaches her in a series of "strides", her location revealed by her tap.

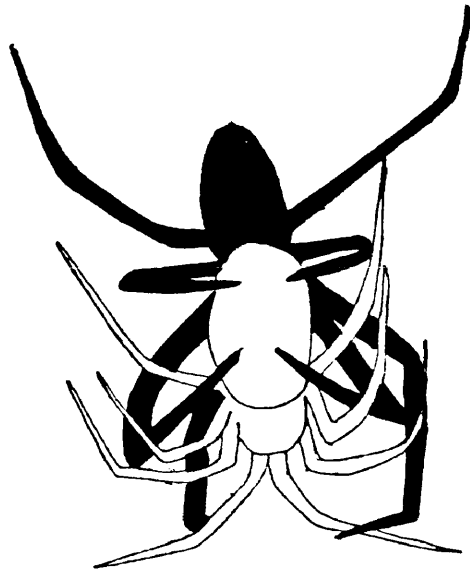
The strides taken by the male are composed of a forward movement, each stride being roughly the length of the male's body. There is also a bobbing of the abdomen, reminiscent of the abdomen bob described by Farley and Shear (1973) for Lycosa carolinensis: "The abdominal vibration consists of two distinct movements. First there is a downward twitch;...the second movement is a vibrating return of the abdomen to its original position." In M. lemniscata each stride is preceded by a tensing of the dome. The stride may also be interspersed with abdominal quivering which is accomplished by the abdomen being very rapidly moved up and down. The female's

reaction to such quivering is to immediately stop all movement. Following this the male approaches closer to the female in his striding fashion. Here the female will, if receptive, tap on the dome with a leg of the first pair, the one closest to the male.

They may or may not engage in leg probing at this point. This involves the first two pairs of legs of each spider touching the partner. The intensity of touching may be great, causing one partner, usually the female, to flee. If this occurs epithalamic courtship must return to a previous step, although not always the first. However, if the partners do not separate or if leg probing is not present and the female is receptive, she will now assume the copulation position (figure 18). In this position, she suspends herself by her fourth legs from the nuptial thread or the dome. The other legs are flexed away from her ventral surface. This allows the male an unobstructed area in which to maneuver into position. The male may, while in close proximity, quiver his abdomen for approximately three to four seconds. The female reacts to this by remaining or becoming motionless. It must be pointed out, however, that not all males quiver their abdomens.

It is found in M. lemniscata that, as in many releaser systems, if the chain is broken the behavior must revert to a previous stimulus in the reaction chain. However, M. lemniscata has the ability to bypass certain previous steps if the sequence is broken. This flexibility in resuming the reaction chain may be explained as possibly energy conserving and therefore might be favored evolutionarily. It also provides the possibility for

Figure 18. Copulation position of Mecyanogea lemniscata. Male is dark and the female is light. Notice the male's use of his legs on the female's abdomen.



abbreviated chains to be developed by a pair of cohabiting spiders. This is shown in figure 15, where courtship behavior may begin at a more advanced stage than nuptual strumming and proceed to copulation. This also allows the courtship sequence to be initiated by the female. The most common starting point for these short chains are leg tapping for the female and "tense dome" for the male. It has been noted on a few occasions that a female will assume the copulation position as soon as a male performs any movements associated with epithalamic courtship. On the other extreme, it has been observed that males have spun up to five nuptual threads, strummed vigorously, and pursued a female without any response on her part, except avoidance.

The flexibility exhibited in epithalamic courtship by M. lemniscata assures copulation in this labyrinthian species.

III. COPULATION

Araneid spiders in general perform lengthy courtship rituals and short copulation sequences (Platnick 1971). Locket and Bristowe (1926) reported that Epeira curcurbitina males perform a "sort of continuous dance" for approximately fifteen minutes before approaching the female. In reference to copulation they continue "...the male reached down and made three applications of the palpi so rapidly that I failed to record the precise relative positions of the spiders." Gasteracantha minax preceeds thread "twanging" by rapid back and forth movements on the outskirts of the female's web for twenty minutes (Mascord 1966). Copulation in this species is reported to last for fifteen minutes, which is relatively long

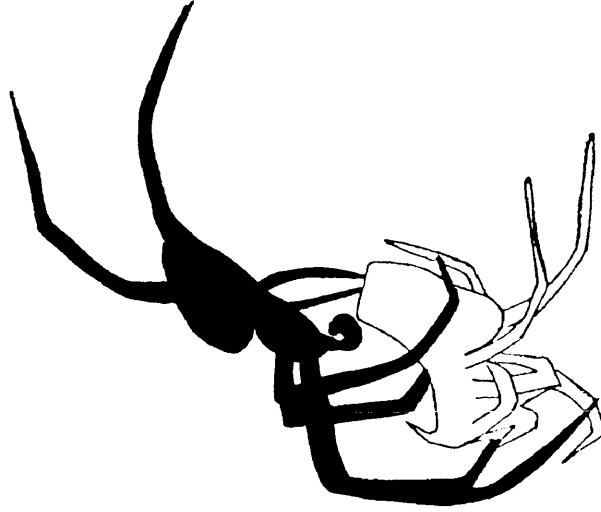
for an orb weaver. Courtship and copulation in the highly sexually dimorphic species, Cyrtophora citricola (Blanke 1972) demonstrates the general rule of araneid behavior emphatically. Courtship begins with the male walking about below the female's dome. He next moves to the dome and makes a nuptial thread. He strums the thread until the female signals to him, which may take considerable time. The act of copulation, however, may last only four to seven seconds, for if the male exceeds this time limit the female treats him as a foreign object and wraps him for food. In Araneus pallidus the female holds the male after insertion of a palp, by a deadly bite; copulation by definition is short.

Unlike many male spiders, the male M. lemniscata appears to be in very little danger during courtship and copulation. This is due to two factors: a) The life style of the species is to cohabit for an extended period of time which necessitates tolerance by both partners, and b) The relative size of the spiders, (the male is only slightly smaller than the female). This size advantage also allows the male to manipulate the female's abdomen with his legs during copulation to insure palpal insertion; whereas, the male of a highly sexually dimorphic species cannot reach the abdomen of its partner without the partner's assistance.

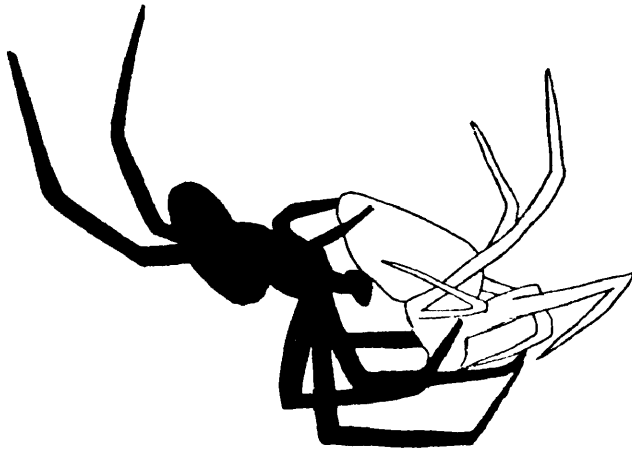
Copulation begins in M. lemniscata when the male maneuvers into position, aligning his cephalothorax with the female's abdomen (figure 19) and positioning his abdomen above hers. The relative positions of male to female differ from species to species. Araneus diadematus utilizes a position similar to M. lemniscata,

Figure 19. Male Mecyanogea lemniscata maneuvering into copulation position. At A the males legs have started to hold back the female's legs and grasp her abdomen, the palpi have not made contact with the female. At B the male has contacted the female's epigynum and is moving into final position.

A



B



while in Cyrtophora citricola the male's body forms a right angle with that of the female. In Araneus pallidus the male's abdomen is directed towards the female's cephalothorax (Blanke 1972).

Male M. lemniscata use their legs to assure a successful copulation. One of his first legs holds back one of the female's first legs, his remaining first leg is positioned between her third and fourth legs and rests on her abdomen. His second leg, on the side opposite the first leg which is holding her first leg, holds back the female's other first leg, while his remaining second leg is positioned between her third and fourth legs and resting on the other side of her abdomen. The male's third legs embrace the female's abdomen (figure 18). In this position the male may manipulate the female's abdomen with his legs and thereby move her epigynum (figure 20) as well as his pedipalps. In this way he has added flexibility to aid in palpal insertion. This flexibility is non-existent in highly sexually dimorphic species, and special adaptations have evolved to aid the males of these species in inserting their palpal organs. Blanke (1972 and 1973) reports that the females of both Cyrtophora citricola and Araneus curcurbitinus use their third pair of legs to change the angle of the nuptial thread so that the male's pedipalps will better align with the epigynum when he climbs along the thread to copulate.

The choice available for a copulation site again demonstrates the latitude of mating behavior of M. lemniscata. Within other species copulation takes place only on the nuptial thread (Uloborus Berland 1914 as cited in Locket and Bristowe 1926, Epeira curcurbitinus

Figure 20. Genitalia of a female. A shows the epigynum of
the female, B points to the gonopore of the female.



Locket and Bristowe 1926, Cyrtophora citricola Blanke 1972, Meta segmenta Blanke 1974). M. lemniscata however, will copulate on the nuptial thread or on the dome.

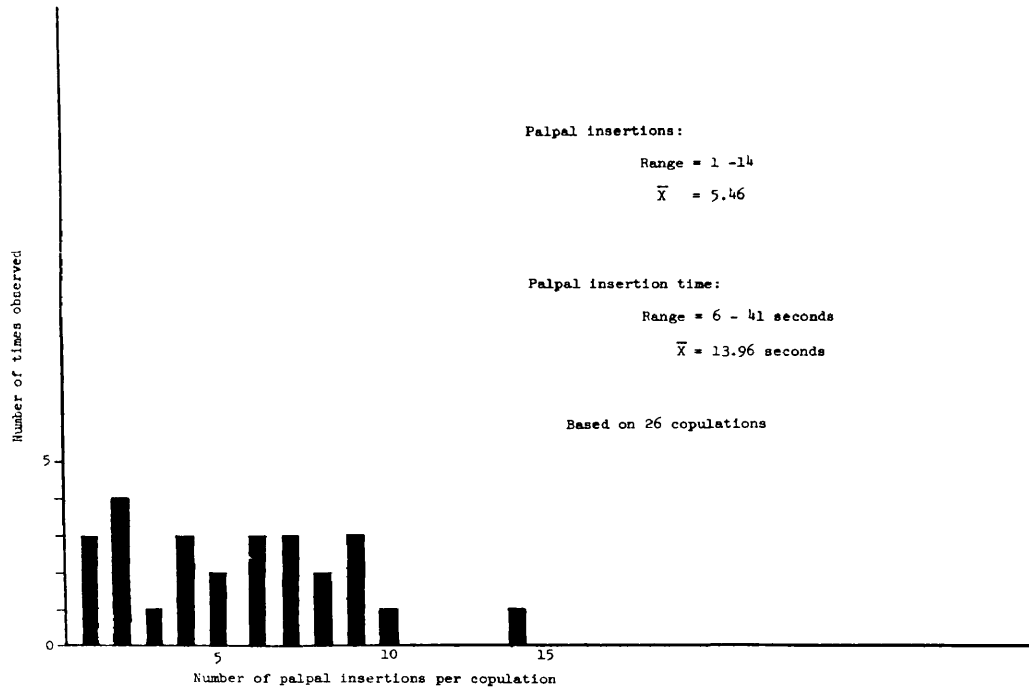
Regardless of where copulation proceeds, once the male is in position he begins to apply his pedipalps, one at a time, to the female's epigynum. How the complicated palpal organ works is not completely understood. The palpal organ is expanded by an increased hemolymph pressure which extends the hematodocha (figure 9)(Kastner 1968). The result is an intromittent organ which transfers sperm into the spermatheca of the female.

In M. lemniscata the number of palpal insertions ranged from one to fourteen (figure 21), the average being 5.46. This is based on twenty-six copulations in which the palpal insertions were counted. The time of a palpal insertion ranged from six to forty-one seconds, the average being 14.13 seconds. The general pattern of palpal applications is to alternate palpi, although this is not strictly adhered to.

A pair may copulate several times in rapid succession. One pair was observed to copulate twenty times in two hours and fifteen minutes. During this heightened copulatory period the releaser system is abbreviated revealing a number of smaller reaction chains.

Copulation generally ends abruptly with each partner moving away from the other. The female makes no attempt to pursue and wrap the male. The termination of copulation may also be lacking in alarm. On several occasions, a male was observed to gently move away from the female after copulation, leaving the female still in

Figure 21. Number of palpal insertions per copulation



the copulatory position. In some species the male is in considerable danger of being killed by the female. Time seems to be the limiting factor, and if a male exceeds a certain time limit during copulation without resuming courtship, the female attacks him. This is true in Cyrtophora citricola as was stated above. Araneus curcurbitinus is also regulated by a time limit for copulation (Blanke 1974), although it is relatively long and a male normally has little difficulty in surviving copulation. Other species have no time limit or the time limit is so long that the females are never seen to attack during copulation. Mascord (1966) states that Gasteracantha minax has a palpal insertion time of fifteen minutes, and that on completion of copulation, the male remains with the female for "a few minutes" before taking his leave. The female remains motionless throughout courtship and copulation and "for several minutes after the male has retreated." It appears that M. lemniscata also enjoys the advantage of copulation without a time limit. The male is never attacked, eaten or driven away from the dome. The male may cohabit within the female's dome for the amount of time necessary to copulate once on up to six weeks.

IV. COHABITATION

As stated above, the male and female of M. lemniscata may live together in the female's dome for up to six weeks. This agrees with what Exline (1948) reported in her study of a population of Allepeira lemniscata (Allepeira = Mecyanogea, Kaestner 1968) in Austin, Texas.

Much of the time during cohabitation the male and female are in the typical stance (figures 1 and 2) hanging motionless from the dome. Both partners feed while cohabitating, but there is no cooperation in prey capture. In fact the opposite was observed on several occasions. The male was seen to chase the female from a fly she had captured, and the reverse was also noted, the female stealing the male's prey. It is interesting to record that the partner is never confused as potential prey during prey capture.

The spiders may mate several times during cohabitation and the males have been observed to perform sperm induction in the course of cohabitation.

Although capable of mating with more than one male if the opportunity presents itself, the female is no longer receptive once she is ready to spin an eggcase, usually in September. Most males leave the web at this time and it is not known where they go.

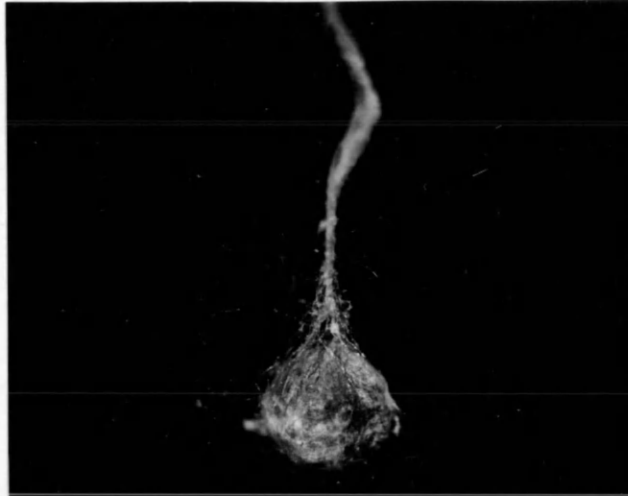
V. EGGCASE CONSTRUCTION

Through the course of August to September the female will spin from one to nine eggcases, the average number being 3.16 (table 6). The actual construction of an eggcase has not been observed, therefore an explanation of its components will be presented in lieu of sequential building steps. The eggcases are nearly spherical, measuring from three to five millimeters in diameter (figure 22). The outside of the eggcase is covered with a fine grayish silk interwoven with small pieces of debris. Underlying this camouflage

Table 6. Eggcases of Mecyanogea lemniscata.

	#	%
Eggcases normal	236	78.7
Eggcases parasitized	64	21.3
Webs normal	65	68.4
Webs partially parasitized	18	18.9
Webs totally parasitized	12	12.6
Total number of eggcases	= 300	
Total number of webs	= 95	
\bar{X}	= 3.16	

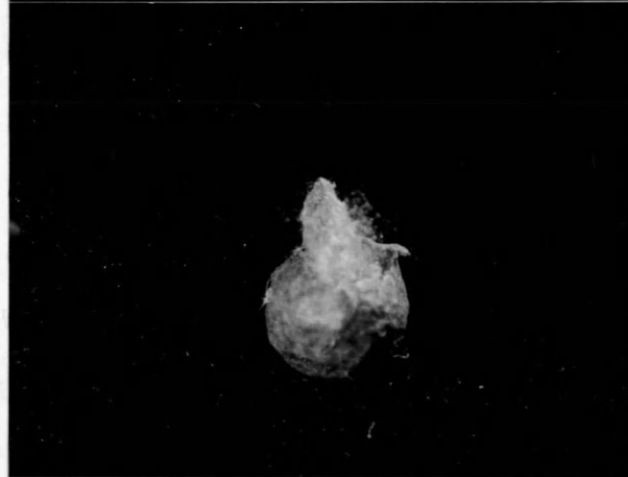
Figures 22 and 23. Eggcase of Mecyanogea lemniscata. 22a shows the eggcase unaltered, 22b displays the eggcase with the outer silk stripped off; 23a shows the eggcase opened to expose the flocculent silk. In 23b the spiderlings can be seen in the silk.



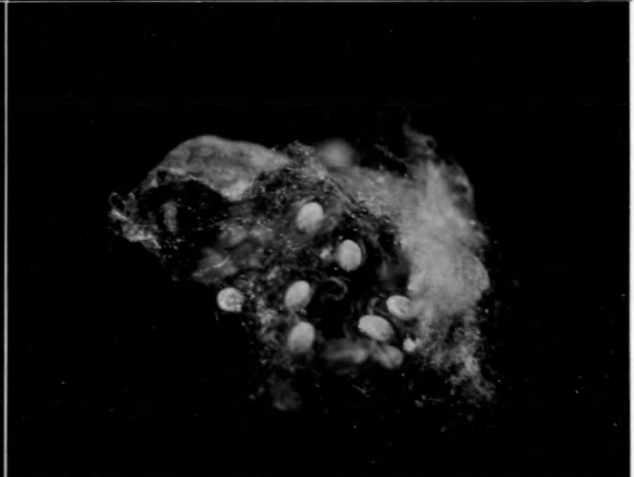
22A



22B



23A



23B

layer is a extremely tough, parchment-like, olive green layer. Exline (1948) states that this covering is waterproof.

The eggs are held together by very fine silk and surrounded by a mass of flocculent silk (figure 23). The number of eggs per case range from five to thirty-five, with the average being approximately fifteen (table 7). Exline (1948) reports that the eggcases contain "a mass of about twenty yellow eggs", and that the average number of eggcases per web is three to five.

The eggcases are deposited in a string, which is suspended by a very strong complex of silken threads formed into a line. This line runs above the hub of the dome and the eggcases hang from it (figure 24).

The way in which M. lemniscata deposits her eggcases is species-specific. This is true for spiders in general as Comstock (1967, p. 208) explains "The eggsac is not merely a covering made in a haphazard way; but is a more or less elaborate structure, made in a definite manner characteristic of the species; it is frequently as easy to recognize the species from a study of the eggsac as it is from a study of the spider herself."

It was ascertained that a female M. lemniscata utilized approximately thirty-one percent of her body weight in the construction of one eggcase. On 6 December 1975 a female M. lemniscata was auspiciously weighed, and on 7 December 1975 it was discovered that she had built an eggcase. She weighed 0.0755 grams on 6 December and 0.0520 grams on 7 December. It is assumed that

Table 7. Number of eggs per eggcase of Mecyanogea lemniscata.

NUMBER OF EGGCASES PER STRING	NUMBER OF EGGS IN EACH EGGCASE					
	1st	2nd	3rd	4th	5th	6th
2	18	13				
5	27	20	16	15	9	
3	11	13	10			
3	8	12	9			
6	25	25	26	15	16	9
3	10	11	7			
4	9	7	12	16		
3	14	14	11			
3	*	11	9			
1	10					
1	5					
2	14	9				
3	21	13	5			
2	10	9				
1	17					
3	20	16	7			
4	25	18	19	10		
3	17	24	9			
3	20	10	10			
3	15	12	17			
4	26	20	35	16		
1	15					
3	17	12	9			
1	20					

*Parasitized

Total eggcases = 67

Total eggs = 1050

\bar{X} number of eggs/eggcase = 15.67

Figure 24. String of eggcases. Eggcases are suspended above the dome by a very strong complex of threads formed into line.



the difference of 0.0235 grams made up the eggs and silk that was used in eggcase construction.

The female remains with her eggcases once they are constructed, touching them with her legs. It is not known if this species displays maternal behavior (i.e., protective behavior for the eggcases).

It was discovered that the eggcases of M. lemniscata are parasitized by an unidentified scelionid wasp (figure 25). Parasitized eggcases are identified by having a hole in the waterproof covering (figure 26). Three-hundred eggcases from ninety webs were examined for signs of parasitism (table 6). Sixty-four eggcases from thirty webs were found to be parasitized. Therefore 21.3% of the eggcases were parasitized affecting 31.6% of the webs. Interestingly enough only 40% (12) of the parasitized webs experienced total loss of eggs, the remaining 60% (18) lost only part of their eggs but not all.

Figure 25. Parasite of Mecyanogea lemniscata. Unidentified scelionid wasp that parasitizes the eggcases of Mecyanogea lemniscata.

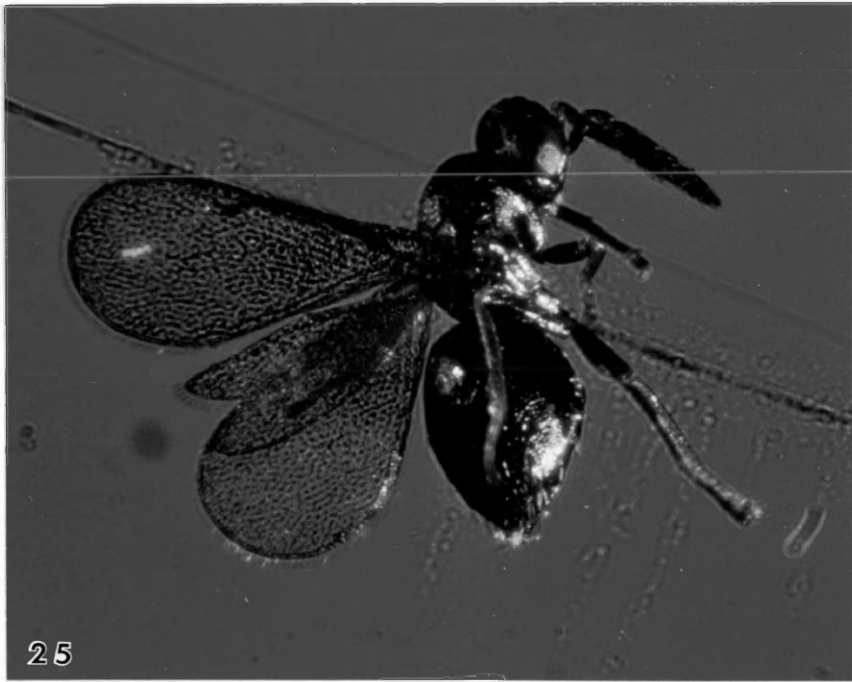
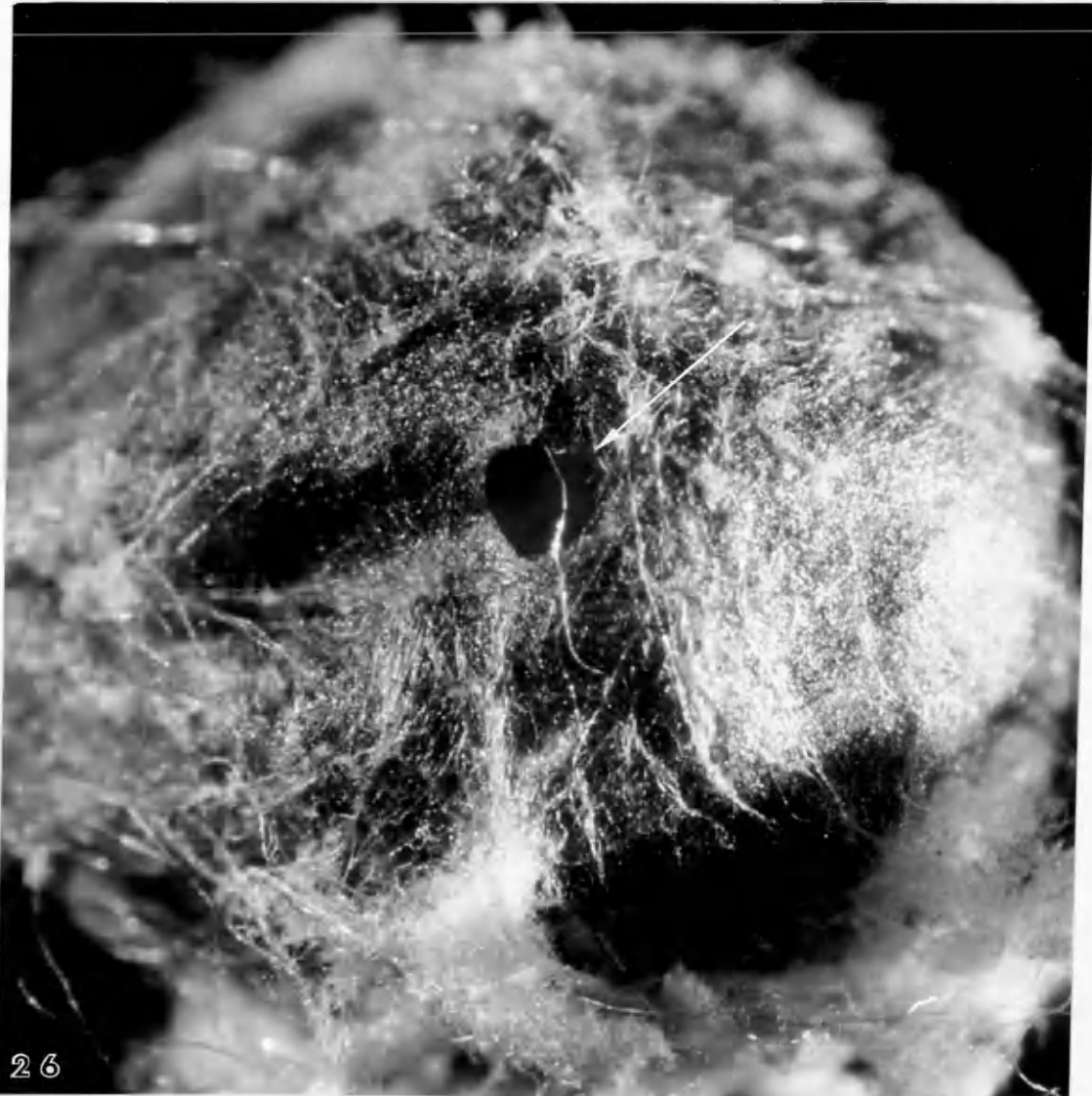


Figure 26. Parasitized eggcase of Mecyanogea lemniscata. Arrow points to hole in the waterproof covering of the eggcase caused by the parasitic wasp.



26



26

CONCLUSION

The sexual behavior of M. lemniscata is complex and displays variations on the general orb web weaver pattern of courtship and copulation.

Male introductory courtship is composed of three types: a) matrix plucking, b) peripheral dome strumming, c) and charging. Males that charge do not utilize either of the other types of introductory courtship. Likewise, males who perform matrix plucking and/or peripheral dome strumming do not charge. This situation raises two interesting points. First, the possibility exists that two behavioral phenotypes are being observed: a) an aggressive phenotype characterized by the charging male and b) a non-aggressive phenotype represented by the matrix plucking/peripheral dome strumming males. Varying degrees of aggressiveness were noted in the females; however, the differences were subjectively evaluated and therefore no conclusive statement may be made concerning them. The possibility exists, nevertheless, for aggressive and non-aggressive type females. These two behavioral phenotypes may be maintained in the population by preferential mating. It can be reasoned that an aggressive male (charger) would experience more success when attempting to mate with a non-aggressive female than an aggressive female. The non-aggressive female would be

more tolerant to his approach. Conversely, an aggressive female would be more likely to tolerate the approach of a non-aggressive male who identified himself. Mating between aggressive males and females would probably have reduced success, and crosses between two non-aggressive partners would be highly successful.

The second possibility may be that the two types, aggressive and non-aggressive, are from two different populations or even two different species. Dondale (1967), while investigating the sexual behavior of Philodromus rufus, discovered that males approach females in two distinctly different ways. "Some males vibrated legs I and II rapidly (the legs appeared blurred to the human eye) upon the female's body, while others tapped slowly with their legs and showed no vibratory movement." He continued to investigate, looking for further ways to distinguish the two types of males. His results showed slight morphological differences (male palpi and body coloration) and more behavioral differences (female oviposition site selection). After applying Dobzhansky's three prerequisites for specific distinctiveness in cross-fertilizing organisms, Dondale declared the two types to be different species. Dobzhansky's prerequisites are: a) the genes producing the isolating differences are multiple, complementary, or at least two in number; b) the genes producing hybrid inviability or sterility are dominant; c) any observed physiological isolation is derived from previous geographic isolation.

In M. lemniscata, to enhance the possibility of more than one species, it is noted that in addition to introductory courtship

differences, males differ in another behavioral aspect. During epithalamic courtship some males approach the female by striding forward while bobbing the abdomen. Others perform this approach by striding forward, bobbing the abdomen and quivering the abdomen. These differences in behavior were not distinguished until the final synthesis of this study, and no interrelationships of the differences were noted as the study progressed. Therefore further investigation is needed in which care is taken to assess sibling behavior patterns to clarify which of the two possibilities, or others, explain the observations presented.

M. lemniscata performs four separate thread vibrating behaviors during mating: a) matrix plucking, b) peripheral dome strumming, c) nuptual thread strumming, and d) thread plucking during sperm induction. It is generally accepted that the web building spiders have poor vision and rely on tactile communication (Montgomery 1910). Both matrix plucking and thread plucking of sperm induction are performed in the matrix of the female's web. Each is relatively slow in frequency (of vibration). The function of both behaviors is identification. Matrix plucking is a type of introductory courtship and therefore serves to alert the female that a male is nearby and not prey. Plucking during sperm induction informs the female that there is a male in the matrix thereby preventing her from entering the matrix and disrupting the sperm induction process.

Peripheral dome strumming and nuptual thread strumming are both performed within the dome and have an increased frequency of vibration as compared to the aforementioned plucking behaviors. The

function of peripheral dome strumming is twofold. It acts as an identification booster, reidentifying the male at the edge of the dome, and begins the sexual stimulation of the female. In this way peripheral dome strumming is intermediate in function, between identification and excitation; and intermediate in position, between the matrix and the hub of the dome; and intermediate in vibration frequency, between matrix plucking and nuptual thread strumming. Nuptual thread strumming is the most rapidly performed vibrational behavior, its function is excitatory, and it is the beginning of epithalamic courtship.

All vibrational behaviors exhibit the same general pattern, although at different amplitudes and frequencies. The general pattern is an oscillation of the vibrational amplitude. It can be reasoned that vibratory behavior executed in the matrix would be required to be slow relative to behavior enacted in the dome. In order to fulfill a communicative function all plucking performed in the matrix would have to relate a species-specific rhythm. If the plucking were produced quickly, it is possible that the complex three dimensional structure of the web could reverberate the signal to such an extent so as to destroy any species-specific rhythm originally imparted to it. This rapid matrix plucking would, therefore, be selected against. A slower, stronger plucking in the matrix would have greater likelihood of transmitting the species-specific rhythm to the female. Tolerance to increased plucking rate increases as the distance to the center of the dome decreases. Thus these behavior patterns may be directly related to the structure of the web.

The influence of web structure on behavior is also expressed by the latitude of response displayed by both male and female in epithalamic courtship. The responses exhibited during epithalamic courtship are not drastic departures from normal (orb weaver) responses at a particular step of the reaction chain. Rather, the variations observed are directly related to the fact that the three-dimensional web of M. lemniscata provides the physical space within which these variations can be performed. Therefore these variations are seen as logical extensions of pre-existing behaviors.

Copulation in M. lemniscata does not appear to be limited by time as in other orb weaving species. Palpal insertions are facilitated by the manipulation of the female's abdomen by the male resulting in a high percentage of successful matings. Females may mate with more than one male and the reverse is also true.

Cohabitation of the sexes in this species would tend to insure successful insemination of the female. It can be taken as circumstantial evidence that the males do not perform sperm induction until in the presence of a mature female. Cohabitation also raises a question concerning aggressive and non-aggressive types. Do aggressive spiders cohabit, and if so for how long? This question points to the need for further study to clarify the status of aggressive and non-aggressive types of M. lemniscata.

The use of many small eggcases by M. lemniscata may be a defense against parasites. Lubin (1974, p. 329) presented the parasite defenses of Cyrtophora moluccensis: "Adult females of C. moluccensis responded to the presence of the fly by violent shaking of the

horizontal net and by climbing up onto the eggcases and encircling them with all four pairs of legs. The latter behavior was accompanied by an agitated waving of leg I, palpating and tapping the eggcase, and plucking the barrier (matrix) web threads around the eggcase. Web shaking and directional responses of C. moluccensis to parasite attacks occur only while the fly was actually flying in or near the web. As soon as it landed in the barrier (matrix) web or on an eggcase, the spider ceased to respond." Parasite attacks on M. lemniscata have not been observed, however, it is possible that their response is similar to the Cyrtophora response since they are related genera. It is obvious, however, that another defense against parasites would be to produce smaller and thus more eggcases. The parasite would then have to find and parasitize several eggcases instead of one.

This initial study of the sexual behavior of M. lemniscata provides needed information and raises many interesting questions for further study.

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