MATING BEHAVIOR OF WATER MITES OF THE GENUS *EYLAIS*[1]

BY

CARMINE A. LANCIANI.

Department of Zoology, University of Florida, Gainesville, Florida 32601.

Species of the water mite genus *Eylais* show a range in mating from a relatively simple process of spermatophore deposition and pick-up to true copulation. Some species show intermediate behaviors that may indicate steps in the evolution of copulation. Natural selection most likely will favor behavioral traits that maximize the proportion of successful matings and minimize the chances of interspecific mating. Copulation appears to meet both of these requirements to a greater extent than do the other forms of mating in *Eylais*, and thus it should be favored by selective forces. This paper describes the major behavioral elements of mating in 18 species of *Eylais* and suggests a possible sequence of events in the evolution of copulation.

METHODS.

All observations were made on recently emerged virgin females. Most pairs mated only if placed in a water filled container with a substrate of fine gravel or algal mats. Gravel and algae apparently provide a more satisfactory surface for spermatophore deposition than do smooth glass walls. Copulating species mated readily in any water filled container. Observations were made with a dissecting microscope at low light intensities, and the specific events were timed with a stop watch. All matings described resulted in the production of large numbers of viable eggs.

CHARACTERISTICS COMMON TO ALL SPECIES.

Whether or not a species copulates, adult mites of both sexes must be brought together before mating can occur. This problem is intensified in species of *Eylais* by the small number of adults in many of the species living in any biotope. A second problem is the presence of other, congeneric species in mating condition, for although the number of individuals in a species may be small, many species often inhabit the same pond at the same time. Thus, the mites should have characteristics that suggest solutions to these problems.

One characteristic noted in all species is the early appearance of males. *Eylais* species are parasitic as larvae on adult, aquatic insects. The larva becomes engorged and metamorphoses

1. Supported in part by National Institutes of Health, Predoctoral Fellowship 5 — F1 — GM — 33, 437. I am grateful to Rodger MITCHELL for his helpful comments on the manuscript.

to the nymphal stage. The nymph leaves the host and feeds as a predator for a period of 1 to 17 days, after which it wraps its legs around a plant stalk or leaf and enters a metamorphic stage, the teleiochrysalis. The adult emerges a few days later. Since males are always smaller on the average than females, they feed less as nymphs, enter the teleiochrysalis sooner, and, as a result, emerge sooner. Related to this phenological trait is a behavioral adaptation that was observed many times in the field and laboratory. Males, alone or in groups, crawl over conspecific females that have not yet left the teleiochrysalis. This behavior increases the likelihood of females being paired after they emerge from the teleiochrysalis. Consequently, the problem of initial contact of mites may be solved by the concentration of mites in zones of the pond containing aquatic plants for teleiochrysalis attachment and by the early emergence of males, which seek out immobile females that are still in the teleiochrysalis.

Morphological and behavioral characteristics of all species of *Eylais* suggest a solution to the problem of species recognition. Before mating, adults show a continuous leg-to-leg and leg-to-body touching between the sexes. Structures that may be important to this behavior are (1) long, fine, leg setae that are set apart from the abundant swimming setae and that may have a sensory function and (2) integumentary glands (STOUT 1953) that may produce species specific substances important in species recognition during mating. In all stages of mating shown by *Eylais*, the male, immediately after first contact with the female, initiates the mating by grasping the female's dorsum or, if the male failed to grasp the female, by crawling or swimming in small circular paths that bring the two mites together again. Since this reaction occurs only after an apparently accidental contact, the stimulus is undoubtedly a tactile one. The female then responds by leg touching with conspecific males. Males show the same behavior, though weaker in intensity, after contacting females of other species. However, mating was never observed between different species because the female did not remain near the male and, as a result, did not crawl over the spermatophores the few times they were deposited under these circumstances.

SPERMATOPHORE DEPOSITION ON AN EXTERNAL SURFACE.

Stage I : In stage I, the female is inseminated after she crawls over spermatophores that were deposited on the substrate seconds before by the male. Since spermatophores are deposited on an external surface before they are picked up by the female, there are at least 2 possible problems that arise. The first is that the female may not find the spermatophores even though they have been deposited in the vicinity. The second is that the spermatophores are exposed to nonspecific females that may pick them up accidentally. Both problems can be avoided if the female is directed precisely over the spermatophores of conspecific males. Stage I species have partially solved the problem of female guidance by leg contact between the sexes while spermatophore deposition is occurring.

Observations : The male, after apparently accidentally brushing against the female, immediately begins crawling slowly over the substrate in small circular paths. The female often shows the same reaction but sometimes remains fairly motionless. If the mites fail to contact one another again, the male's searching activity weakens, and it swims away. If the mites again contact each other, the female crawls over the male's dorsum or merely touches his legs. The male, either immediately or after crawling over the female, begins depositing spermatophores as he moves in small, circular paths over the substrate. While depositing a spermatophore, the male lowers his venter to the substrate, rocks his body about a point at his genital opening, and

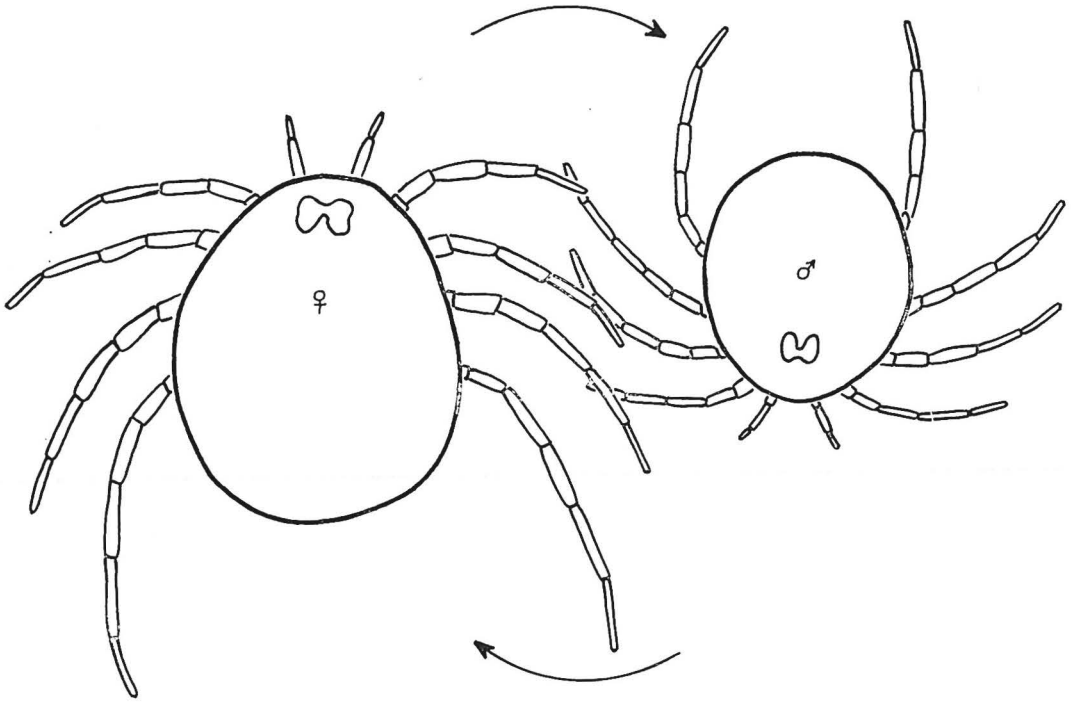

FIG. 1. — Male and female of stage I species crawling in circular paths over the substrate. Leg touching enables the mites to maintain contact and directs the female over the path taken by the male as he deposits spermatophores.

raises the posterior part of his body just as the spermatophore is extruded. The movements of spermatophore deposition in *Eylais* are very similar to those of *Hydryphantes ruber* (MITCHELL 1958). While the male is depositing as many as 20 spermatophores, the female is maintaining contact by leg and body touching. Leg touching is a simple behavioral trait enabling the female to follow the exact circular path taken by the male provided the touching legs are on the same side of the body of both mites (Fig. 1). If the male moves clockwise, the mites keep in contact legs on the right side of the body, and if counterclockwise, they keep in contact legs on the left side of their body. As a result, the female passes directly over the spermatophores, and she picks up one or more of the heads in her genital opening. The entire sequence usually lasts less than 2 minutes after which the mites separate and remain motionless except for a thrashing movement of their third pair of legs. Females examined at this time usually have at le ast one spermatophore head protruding from their genital openings. Species showing this type of mating behavior are *E. brevifurca, E. rectisulcus, E. vernalis, E. coptotomi, E. harmani, E. mitchelli, E. peltodytis, E. parviporus, E. conformis, E. helophori,* and *E. hydraenae.* In *E. brevifurca, E. vernalis, E. peltodytis, E. parviporus,* and *E. helophori* some mating pairs show an additional feature of maintaining contact with legs on both sides of the body. After their initial contact, the mites align but do not touch venters while oriented in opposite directions. With leg tips touching, the mites flail their legs and are propelled through the water in circular paths around a point between their venters. Sometimes several filaments of algae are trapped between their venters, and the male deposits spermatophores on them. Other times the spermatophores are merely extruded between the mite venters and stick together in a tangled mass. The mites then crawl

over the algae clump or the tangled spermatophore mass while still touching the tips of each other's legs, and the female picks up some of the heads in her genital opening.

Stage II : In this stage, the beginning of the pairing tendency is shown. The female is again inseminated as she crawls over spermatophores that were previously deposited by the male, but before this takes place, the male mounts the female. The greater degree of body contact resulting from mounting undoubtedly reduces the probability of interspecific mating.

Observations : In stage IIa, the male responds to an accidental brushing against the female by quickly wrapping his fourth pair of legs around the posterior part of her body. The mites are oriented in the same direction with the male on the female's dorsum and are propelled by the swimming of the female. The mites may separate and rejoin several times until the male eventually crawls from the female's dorsum to her venter. Now the mites not only are oriented in the same direction but also are touching venters, although genital openings are not aligned. The palps of the male move almost constantly and often touch the female's venter in the genital area. After being carried for 7 to 15 minutes by the periodically swimming female, the male crawls a few millimeters away from the female where he deposits in one minute or less 10 to 20 spermatophores on the substrate. The spermatophores are deposited close together and usually adhere to one another by parts of the stalks. As before, the male moves in circular paths as he deposits them. The female which may or may not have crawled over the male before he began, now maintains contact with the male by leg touching as in the first group of mites mentioned. As she follows the male she passes over the spermatophores and picks up some of the heads in her genital opening. After successful mating, the mites separate either immediately or after the male again briefly holds on to the female's dorsum. The sole species in this stage is *E. falcata*.

In stage IIb the male mounts the female but does not crawl around to her venter. Also, instead of maintaining leg-to-leg contact during spermatophore pick-up as do males of species in stages I and IIa, males of species in this stage remain mounted atop the female as she crawls over the spermatophores. This trait may represent an improvement in the efficiency of successful sperm transfer because the male cannot lose contact with the female while she crawls over the spermatophores and therefore, he has an opportunity to deposit several more spermatophores after the female ceases to crawl over the previously deposited ones.

Observations : After brushing against the female, the male either immediately holds onto her dorsum by curving his fourth pair of legs around the posterior part of her body or crawls over her dorsum several times before holding on. With the male atop the female and the mites oriented in the same direction, the female begins swimming for as long as 10 minutes while the male remains motionless except for a beating of legs II and III. The female then stops, and the pair remains on the substrate. The male crawls from her dorsum, deposits usually 2 but sometimes 1 or 3 spermatophores close to and directly in front of the female, and returns quickly to his original position on her dorsum. The female usually remains in place until the male returns and then crawls over the spermatophores several times in small circular paths as she touches the substrate with her palps. After this, the female swims away briefly and after she stops, the male again crawls off to deposit spermatophores. The entire sequence is repeated 2 or 3 times. Each deposition period lasts only about 8 seconds, but the mites may remain together for 30 minutes because some periods are separated by several minutes. In some of the species of this group, the male, while atop the female, moves forward and touches the anterior part of her dorsum and her mouthparts with his legs and palps before he crawls off. Species showing stage IIb mating behavior are *E. ovaliporus*, *E. major*, and *E. glandolosa*, all of which parasitize beetles of the family Hydrophilidae (LANCIANI 1970).

Spermatophores of species in stages I and II consist of a stalk, a base (which is merely the lower part of the stalk bent at an angle on the surface of the substrate), and a dorsoventrally flattened head which contains sperm. Most spermatophores bear several, long, hairlike extensions from the middle of the stalk. The spermatophore stalks vary in length from 0.2 — 2.0 mm and in width from 0.03 to 0.10 mm among the species. The heads are from 0.08 — 0.26 mm long and 0.05 — 0.18 mm wide.

Copulation.

Stage III : The first few steps in the premating behavior of the species of stage III are similar to those of *E. falcata*, the species of stage IIa. The great degree of body contact most likely reduces the probability of interspecific mating, and the internal deposition of spermatophores effectively increases the efficiency of sperm transfer.

Observations : Böttger (1962) described the mating behavior of *E. infundibulifera*, one of the species considered in this study, and my observations are similar to his. In these species, after a male and female meet accidentally, the female falls to the substrate and stretches her legs apart away from her body. The male, which usually holds on to the female's dorsum briefly, then assumes the pairing position on the female : venters touching, external genital openings aligned, bodies oriented in the same direction, and leg IV of male holding the pair together by curving around the posterior end of the female and up on to her dorsum. All other legs of both mites are held away from the body. Leg III of both mites is raised vertically and moves in the typical thrashing manner. After this position is assumed, the female begins and periodically continues swimming movements that are strong enough to propel the copulating pair. By separating pairs at different times after the onset of copulation, Böttger (1962) was able to determine that sperm transfer occurs within the first 4 or 5 minutes, even though pairs may stay together for 1 to 2 hours. Two species of this stage are *E. discreta* and *E. infundibulifera*. *Eylais belostomatis* also copulates but shows 2 differences from the other 2 species. The female does not always stop immediately after brushing against the male but continues swimming, carrying the male on her dorsum. When she finally stops, the male crawls around to her venter and copulation follows. Also the entire copulatory act, during which the male often rocks from side to side, lasts only 2 to 5 minutes. Thus, the long period after sperm transfer during which the pair remains together in *E. infundibulifera* is not seen in *E. belostomatis*. Stout (1953) observed copulation in *E. waikawae*, which parasitizes Hemiptera. In this species, the male and female are oriented in opposite directions and may remain together for as long as hours. The species that copulate are similar in their host preferences. All three of them parasitize species of aquatic Hemiptera : *E. infundibulifera* and *E. discreta* parasitize corixids and *E. belostomatis* parasitizes belostomatids (Lanciani 1969).

Discussion.

The different mating behaviors can be summarized :

I. Initial contact ; deposition of spermatophores ; pick-up of spermatophores,

IIa. Initial contact ; mounting ; alignment of venters ; disbanding of coupled position ; deposition of spermatophores ; pick-up of spermatophores,

IIb. Initial contact ; mounting ; dismounting ; deposition of spermatophores ; mounting ; pick-up of spermatophores,

III. Initial contact ; mounting ; alignment of genital openings ; copulation.

The sequence of mating stages I, IIa, and III involves an increasing amount of body contact and culminates in copulation. The one species of stage IIa shares characteristics with species of stage I and III, and thus, IIa could represent an intermediary stage in the evolution of copulation from external spermatophore deposition. Stage IIb species show the same mounting behavior as stage IIa and stage III species but the females in this group behave differently during spermatophore contact in that they carry the male on their dorsum. Thus, stage IIb appears to be an offshoot of stage IIa and not in direct line to stage III. If this is the true evolutionary sequence, it must be shown that copulation is a more advantageous means of insemination. As noted above, copulation does appear to be more satisfactory to the species because it reduces spermatophore wastage and, because of the greater amount of body contact, it most likely reduces the problem of interspecific mating. However, external spermatophore deposition is apparently an adequate form of insemination since it has been maintained in species of stages I, IIa, and IIb. Certainly the form of insemination shown by species of these stages is a more efficient utilization of spermatophores than that shown by another water mite, *Hydryphantes ruber*, in which the males deposit large numbers of spermatophores in the absence of females (MITCHELL 1958).

In the non-copulating species of *Eylais*, the deposition of spermatophores only after the male and female have contacted one another increases the efficiency of sperm transfer. Species of stages I and IIa further increase this efficiency by leg touching behavior, which guides the female over the newly deposited spermatophores. In species of stage IIb, the female does not follow the male over the spermatophores, but spermatophore wastage is minimized because the male deposits only a small number of spermatophores at one time and then returns to the female's dorsum. If the female picks up a spermatophore in her genital opening, the mating has succeeded. If the female fails to pick up one of the spermatophores produced in the first deposition period, she most likely will have several more chances immediately since the male is readily available on her dorsum. On the other hand, in species of stages I and IIa, contact is sometimes broken between the leg touching mates before a spermatophore has been picked up by the female, and, as a result, insemination cannot occur in that episode despite the fact that as many as 10 or 20 spermatophores have been deposited. The two mites then must again rely upon random encounters to initiate mating. Thus, in species of stage IIb, the evolution of mounting interspersed with several brief deposition periods during each of which only a few spermatophores are produced may have simultaneously conserved spermatophores and promoted a greater likelihood of successful insemination.

Copulation in species of *Eylais* appears to be a more efficient system of insemination than external spermatophore deposition, and, therefore, it is logical to assume that copulation has evolved from the condition of external spermatophore deposition. The latter is nevertheless a successful means of insemination as a result of the adaptive modifications in behavior that serve to maintain contact between the sexes during the period of spermatophore deposition and pick-up.

LITERATURE CITED

BÖTTGER (K.), 1962. — Zur Biologie und Ethologie der einheimischen Wassermilben *Arrenurus* (*Megaluracarus*) *globator* (Mull.), 1776 *Piona nodata nodata* (Mull.), 1776 und *Eylais infundibulifera meridionalis* (Thon), 1899 (Hydrachnellae, Acari). — Zool. Jb. Syst., **89** : 501-584.

LANCIANI (C. A.), 1969. — Three species of *Eylais* (Acari : Eylaidae) parasitic on aquatic Hemiptera. — Trans. Amer. Microsc. Soc., **88** : 356-365.

LANCIANI (C. A.), 1970. — New species of *Eylais* (Acari : Eylaidae) parasitic on aquatic Coleoptera. — Trans Amer. Microsc. Soc., **89** : 169-188.

MITCHELL (R.), 1958. — Sperm transfer in the water-mite *Hydryphantes ruber* Geer. — Amer. Midl. Nat., **60** : 156-158.

STOUT (V.), 1953. — *Eylais waikawae*, n. sp. (Hydracarina) and some features of its life history and anatomy. — Trans. Roy. Soc. New Zealand, **81** : 389-416.