This is a PDF version of PECKHAMIA 1(4): 63-70, March 1978. Pagination of the original document has been retained. Author's note (24.1): *Eris marginata* is presently called *E. militaris*. *Phidippus rimator* (now *P. clarus*) is no longer in use. The *Icius* and *Metaphidippus* referenced here are presently known as *Tutelina* and *Pelegrina*, respectively. An updated, illustrated version of this document (24.2) will be published with 24.1.

THE BEHAVIOR OF *ERIS MARGINATA* (ARANEAE: SALTICIDAE). David Edwin Hill

Eris marginata is the most conspicuous of the jumping spiders inhabiting blackberry bushes (*Rubus*) in the vicinity of Corvallis, Oregon. Although the larger salticid *Phidippus johnsoni* occasionally ventures out upon the lower leaves of a blackberry bush, *E. marginata* is the largest jumping spider to consistently appear in this habitat. Several species of *Metaphidippus*, as well as an *Icius* which is probably not described (covered with light blue scales) are also common in blackberry bushes in this area.

The following "ethogram" is distilled from more than 1160 minutes of observation of more than 25 individual *E. marginata* on blackberry bushes, conducted between the 7th and 12th of May, 1975. In Corvallis, the seasonal life history of this species compares with that described for the same species in Nova Scotia (Dondale 1961), on the opposite end of the continent. The period of observation encompassed a portion of the early mating season of these annual spiders, when the males are adult and the females penultimate. Thus, while there are data on the behavior of the adult males, there is no information here on the brooding behavior of the females.

Throughout the period of this study, individual spiders were observed continuously for varying periods of time ranging up to more than three hours. By remaining relatively still, the influence of the observer upon the behavior of the spiders was minimized. Observations were facilitated by a combination of mild climate and a complete lack of biting insects. None of the encounters with either prey or with members of the same species were arranged. Although only a limited number of encounters can be encountered in turn by the observer with this technique of noninterference, the authenticity of the context of undisturbed behavior is desirable.

Diurnal activity patterns. The life of *E. marginata* is greatly regulated by warmth and sunshine. The spiders generally travel on the upper, illuminated surfaces of blackberry leaves and stems. They often move into the sunshine when feeding upon prey. In the morning these spiders, emerging from their shelters, flatten themselves along a leaf or stem in a normal orientation to the solar radiation, perhaps to maximize the effect of the irradiation. When "sunning" in this manner, the appendages are held close to the body and the spider moves little. The dorso-opisthosomal situation of the heart may greatly facilitate the rapid distribution of heat throughout the body of the spider. In this regard it is significant that the opisthosoma may be pivoted to bring the dorsum to face the sun more directly. *Eris* appear to be most active in the mid-day heat. It is at this time that most active travel and exploration takes place. It should be noted that the diurnal activity pattern of this species may be quite different in a different part of the United States. The Willamette Valley of Oregon cools quickly as evening approaches, and when compared to other areas, the mid-day "heat" is really rather mild (perhaps 20C).

In the early evening, long before nightfall, *Eris* begin to construct and occupy shelters between adjoining blackberry leaves. The spiders remain in these shelters throughout the night, and emerge the next day only if the weather is favorable. As the air cools in the evening, the spiders often may be seen "sunning" as in the morning.

Locomotion. *Eris* walk slowly about in their shelters in the evening, if they move at all, and are quite sluggish until they have warmed up in the morning (unless threatened). The spiders are only active when the warmth and illumination are favorable, and it is thus that these spiders, particularly the

vagabond males, engage in the greatest amount of travel in the middle of the day. Like other jumping spiders, *Eris* employ at least five basic methods in their movement upon vegetation. Most of the time they are walking at various speeds (or running), with pretarsal foot pads in contact with the surface. They often jump to a sighted target position. They may descend (rappel) on a dragline, or climb a vertical dragline. Finally, like many other spiders, they can construct and climb on the underside of a horizontal bridge of silk, or similarly use a thin plant stem as a bridge.

Eris walk almost equally well on the underside of a leaf or stem as they do on the top, although they use the upper surfaces most often. In addition to the usual forward advance, *Eris* are quite capable of side-stepping and walking backward at variable speed. They often side-step (lateral movement) quickly to a concealed position on the underside of a stem or leaf when threatened by an observer moving overhead. Beyond the basic patterns of walking and other forms of movement, there are no real stereotyped sequences. Thus a jump may precede another jump, or a run, or a series of slow turns. The sequence in which each element of the locomotory repertoire is employed is largely determined by the environs. Thus, if a spider can reach between two leaves, it may continue a walk. If not, it may jump, or turn to reach another object. Movement involves continuing interaction with the immediate possibilities.

The most commonly employed walking pattern may be termed an *exploratory walk*. In this walk the spider takes a variable number of steps, then stops, then takes a few more steps, then *stops*, and so on. After several intervals of this pattern, the spider

may *pause* to survey the environs systematically, pivoting the prosoma to orient the large anterior medial eyes (AME) in various directions. Information received during this pause may lead the spider to alter its course completely (see below). Periodically, during a pause or long stop, the omnipresent dragline, a strand of strong silk continuously released by the moving spider, is secured to the substratum with an adhesive attachment disk. Although this forward walk is characterized by steps, stops, and pauses, the actual pattern is quite variable, as is the speed of the moving spider. A fast moving spider running along a main stem may take many steps between stops, and may turn quickly to face each of several different directions only briefly during each infrequent pause. A slower spider may take only one or two steps before pausing and surveying systematically in all directions for a prolonged period of time. Again, a fast moving spider may enter a slower, exploratory phase of behavior at any time. Thus a male running along a stem may encounter an object of visual interest, such as a moving insect, and will subsequently move very slowly with frequent turns to survey the environs. Beyond basic feedback from proprioceptors, complex visual stimuli are critical determinants of the pattern of locomotion.

The actual stepping pattern consists of a loose alternation of legs I and III with the ipsilateral legs II and IV, and contralateral legs I and III (see Land 1972). Pedipalps are often moved up and down, although this activity is not restricted to a period of forward locomotion, but also occurs during each pause. In what is perhaps an anthropomorphic sense, one might interpret this "pedipalp flicker" of salticids to be indicative of the state of general excitation of these animals. The legs I are frequently raised in the air and flexed at the junction of femur and patella in a sort of "gesture." Infrequently the walk becomes a relatively slow, continuous but "jerky" (with many brief stops) advance. This pattern of jerky walk is as distinctive as it is difficult to describe. Similar behavior has been observed in several other salticids, including *Phidippus*.

The jump of *Eris*, like that of other salticids (Parry and Brown 1959), depends primarily upon force exerted against the substratum by legs IV. *Eris* jumps clumsily and inaccurately between grass blades which are generally too weak to support this thrust. On blackberry leaves, *Eris* often walk backwards to secure a foothold for the jump. Each jump is preceded by visual examination of the target object with the AME. The spider crouches and flexes legs IV at the tibio-metatarsal joint, and raises legs I and II (flexed at the femur-patella joint) to receive the new surface. Just before each jump, the opisthosoma pivots to bring the spinnerets into contact with the substratum, and the spider releases an adhesive mass of silk to form an attachment disk for the dragline. When a jump is missed, the spider hangs by the dragline and is thus able to recover to its former position. A jump involves the exertion of a calculated thrust to project the spider upon a ballistic flight for the required distance, which may involve 1-20 cm of horizontal flight. In the course of this trajectory the spider may rotate as much as 180^{0} to receive the new surface, although much of the turning may actually take place during the landing itself. Thus *Eris* may leap up to the underside of a leaf from the top of a lower leaf. Most jumps are unerring in their accuracy, even if made in rapid succession.

While a missed jump may result in a sort of (unintended) dragline descent, at times *Eris* will secure an attachment disk and then descend (rappel) on the dragline to a lower position. The spider can stop at any time during the descent, and may then either continue the descent or turn to climb the line and recover the original position.

Eris may ascend either a newly-formed or a pre-existing vertical dragline very quickly, utilizing a characteristic vertical climbing behavior (found in many spiders) involving the handling of silk strands alternately by legs I and II, with legs III and IV outstretched. During this ascent, the silk line is wound into a ball which is immediately discarded as the spider attains its objective.

A very distinctive pattern of travel involves the formation and use of a bridge by *E. marginata* to move between plants. I have observed essentially the same behavior in *Sassacus papenhoei*, but never in any *Phidippus*. Beginning at a vantage position at the end of a stem or at the top of a plant, the spider first descends 5-10 cm on a dragline, then ascends very quickly (vertical climbing behavior) to assume a position on the underside of a leaf edge or stem with the opisthosoma stretched into the air. This positioning is quite distinctive, as there is virtually no pause between the descent and subsequent ascent of the dragline by the spider. Several strands of silk are then ballooned with the wind, and within a minute or so these are almost invariably attached to an object roughly at the same elevation in the vegetation as the spider. The spider then turns and pulls in the slack on the bridge with legs I, perhaps testing for attachment. Then the spider climbs quickly along the underside of this horizontal bridge, using all legs in what probably corresponds to the normal stepping pattern, to attain its destination. It is of interest that a brief descent on the dragline invariably precedes the formation of a bridge. It is likely that this behavior is necessary to draw out the initial strands of silk to such a length as may be captured, and subsequently drawn out, by the wind itself. As noted above, the descent which precedes the formation of a bridge is distinct from the rappel, in that the former involves a rapid turn to ascend *without* pause.

Eris can also employ natural bridges, such as a thin stem, or the silk lines which have been laid down by other spiders. The traversing run in these cases

is like that employed by the spider upon a bridge of its own design. It should be noted that bridging behavior (with silk) is utilized by many spiders to facilitate movement upon vegetation, in addition to the Salticidae.

At times individual *E marginata* appear to wander greatly, without apparent destination. They may also, however, maintain a fairly steady course when moving through vegetation. While maintaining such a course, the animals may periodically stop to survey an elevated (highly visible horizon marker) "objective" plant, then continue the advance. Thus they may travel more or less directly

toward what may be a rather distant goal. At times the spiders consistently ascend as they climb or jump from leaf to leaf. Often they will survey a position with the AME, and then employ an indirect route to attain that sighted position, as necessitated by the arrangement of branches and twigs. Visual survey plays a primary role in the determination of a course by *Eris*.

Sensory activity. *Eris* constantly use the front eyes (AME, ALE) to survey the environs during periods of activity, as noted above. During pauses, the spiders can employ a series of small turns of the prosoma to survey the surroundings. They may turn directly toward each of several nearby leaves in succession, perhaps indicating that the lateral (ALE and PLE) eyes may be capable of directing movement toward a stationary object. The AME and ALE are brought to bear upon an object by turns of the prosoma, which can be turned through a small angle without stepping. In addition to lateral movement, the front of the prosoma (face) may be raised to look up, or lowered to look down. *Eris* will turn to face moving objects (of sufficient size) at distances ranging from several mm to more than 10 m. It is well known that the AME of salticids are utilized for the detailed evaluation of the form of potential prey, but the most extensive use of vision by *Eris* and other salticids probably involves the evaluation of the immediate surroundings and the determination of a course of movement through the vegetation. These spiders are remarkably alert, and the accuracy of each turn to face a stimulus is remarkable. *Eris* will observe an "interesting" object, such as a hunting wasp or a human, for a prolonged period of time without moving.

In addition to the visual sense, *Eris* display a great deal of tactile sensitivity. The forelegs in particular are often tapped against the surface. In addition the pedipalps are frequently brought to touch the underlying plant. This behavior may facilitate the role of chemosensory as well as mechanosensory setae.

Predation on insects. *Eris* jump directly upon sighted prey, generally small insects, which are encountered during a journey through the vegetation. If the prey are detected at more than 1-2 cm distance, the spider may creep slowly toward the prey with pedipalps flickering up and down, to jump at a distance of 1-2 cm. These spiders will also hurtle themselves into the air in pursuit of flying insects. The predatory jump is similar to the locomotory jump, apart from the grasping behavior with chelicerae and legs I and II which is included in the former. The attack is preceded by formation of an attachment disk.

When the prey is held securely, after initial maceration or mastication with fangs and chelicerae, *Eris* carry the prey to a feeding position. In the evening, spiders may carry the prey into the shelter to feed. At mid-day, a feeding spider may move into a sunny position with a good view, such as the top of a leaf or stem. When feeding, the spider crouches against the substratum, holding the legs against the body. Fluids are rhythmically pumped in and out of the prey. *Eris* occupy the better part of an hour feeding on a small

insect, such as a leafhopper, although the time of feeding on even a particular prey item is quite variable. Subsequently the remnants of the prey are dropped and the spider grooms in place by rubbing the pedipalps in loosely alternate fashion over the front of the chelicerae.

Grooming. As mentioned above, the chelicerae are fastidiously groomed after each feeding. The chelicerae are also rubbed against the pedipalps at other times. The pedipalps may on occasion be rubbed against each other as well, or used to groom the first leg. The hairy pedipalps function as the vertebrate eyelid or nictitating membrane, to brush the vital AME clean. The lateral surfaces of the legs and pedipalps may be brushed against the substratum, or against adjacent appendages. At times, any of the leg tips, including each pretarsus, may be cleaned between the endites and chelicerae. This grooming may facilitate the efficient adhesion of these structures, perhaps as the preening of a bird contributes to flight (see Hill 1977). Grooming occurs during a pause in activity. It is commonly seen when the spider is resting (so to speak) in a shelter or concealed position. Extensive grooming follows feeding, but it may also occur after a brief pause during a journey. A spider walking along a stem may pause, turn in several directions, clear the tip of a rear leg between the endites, and then continue the walk.

Non-predatory relations with other species. *Eris* orient toward any moving objects within their field of vision, whether these are butterflies flying 3 m overhead, or mites crawling upon the immediate surface at a distance of only a few mm. Certain observations by the spider, such as the wasp mentioned above, elicit a prolonged interest by the spider. *Eris* will flee from small ants, a behavior which may be related to the fact that these ants will run directly toward the jumping spider (prey is not supposed to do this). *Eris* exhibit no interest in moving ants as prey, nonetheless. By comparison, the much small *Icius sp.* mentioned above have been observed feeding on the same ants a number of times. This subject certainly deserves additional study.

Large vertebrates, such as man, elicit flight and concealment as they approach this jumping spider, particularly when overhead. It has been the practice of this observer to remain low in the vegetation to the greatest extent possible, as a consequence. When sufficiently distant or unobtrusive, however, such large creatures may be observed by the jumping spider for an extended period of time.

Intra-specific relations. Mature male *E. marginata* respond to the recognition (at distances of 10-20 cm) of other members of their species, whether male or female, by engaging in a distinctive series of postures which comprise a sort of courtship dance. This is comparable to the visual display described for other salticids (see Crane 1949, Richman 1977). In this dance the male faces the object of attention, raises and extends the forelegs at a wide angle, holds the body well above the substratum, lowers and turns the opisthosoma to the side, and periodically side-steps in either direction while flexing the extended forelegs rhythmically at each tibio-metatarsal joint .

Most penultimate females and males flee from this performance, and the courting males pursue them until out of sight. At this point the pursuing male will stop and continue the display while turning to face each of several directions in turn. Where adult females cannot escape in the laboratory, this performance is generally a prelude to mating.

Upon recognition, females and males tend to flee quickly from members of the same sex. When courted by a male, an unwilling female may run up to face the

male, and then strike his outstretched forelegs with her own repeatedly. Armed with sharp spines, the forelegs of a salticid (like those of a thomisid) can be formidable weapons to a creature of similar size.

In both *E. marginata* and *Phidippus rimator* (preferably called *P. clarus*), males may cohabit with either penultimate or adult females, in the resting sac. The male may occupy a chamber directly below that occupied by the female. In this case there is a certain amount of interaction between male and female, including the vibration of the silken floor of the chamber inhabited by the female, which serves as a partition between the two spiders. When not aligned below the body of the female, clinging to this silk partition, the male is often vigorously adding strands of silk to all parts of the shelter. Except for the sac of the female, which is probably the molting sac used for the final molt, this cohabitation shelter is much like the ordinary shelter used by *Eris* dwelling upon blackberry bushes.

At this point it is probably worthwhile to interject several comments with reference to subsequent observations of cohabitation in a related but undetermined species of *Eris* at Newnan's Lake, Alachua County, Florida (October of 1977). The males of this smaller species also inhabited sacs beside those of the penultimate females, and this behavior was observed for at least five different pairs. In one case the male was seen on patrol below the resting sacs, and it subsequently attacked a relatively enormous *Tetragnatha* which had dared to venture near the nuptial quarters. In response to the stabs of the forelegs of this small spider, the larger intruder was quickly driven away. This singular observation shows that the territorial defense of cohabiting males is not restricted to members of the same species in application. John Anderson observed four instances of male/female cohabitation for *P. otiosus* (or *P. pulcher* Walckenaer) in the same locality at about the same time. In three of these instances, the male came out first as the sac was disturbed.

Use of shelters and concealed positions. Occasionally a spider will rest under a leaf in a concealed position. *Eris* display a great deal of interest, particularly in a tactile sense, in rolled leaves and the spaces between adjoining leaves. This may be one way of finding prey, but it may also relate to nesting behavior. In the evening, a spider may occupy such a position between two adjoining (overlapping) horizontal leaves or leaflets, and will attach silk strands between the two leaves, thereby forming a shelter or primitive resting sac. Thus a shelter may consist of only two leaves and a relatively small number of silk strands joining the two leaves to define two exits for the spider.

A second level of shelter complexity (and investment) involves the formation of a loose silk platform above the lower leaf. A spider resting on this shelter platform is thus protected from rain water coursing over the lower leaf. During periods of inclement weather *Eris* may remain in the shelter, continuing to add to its structure at intervals [from time to time]. This behavior, involving a variable investment of silk in the shelter, appears to be of adaptive value in western Oregon, where the weather on a given day is usually the most reliable indicator of the weather on a subsequent day. Finally, a sealed sac of compactly woven silk may occupy the top of the shelter, beneath the top leaf and above the horizontal platform. This is most likely utilized as a molting or brooding sac.

The deposition of the individual silken strands which comprise the shelter can be a fairly continuous activity, with stops to attach each strand and on occasion longer pauses or inactive periods. At times the spider may remain at one of the exits, looking out. At other times the spider appears to be testing

the construction, walking and turning within the shelter, and often tapping the silk with the forelegs. When attaching the silk or pulling out a strand between two attachment points, the opisthosoma is raised or lowered and pivoted with great agility, even grace. The six spinnerets weave in their fashion like so many small and agile fingers. During the phase of shelter construction *Eris* will still venture out onto nearby leaves to capture prey should the opportunity arise, but will remain in the vicinity of the shelter. Subsequently the spider can relocate the shelter directly, even though its position may be obscured by leaves. The spider definitely has a memory of the locality, although the extent of this memory remains undetermined.

In favorable weather, with warmth and sunshine, *Eris* emerge to become wandering nomads until late afternoon or evening, when a new shelter must be constructed.

Discussion. The acute vision provided by the AME of these spiders is most often employed in survey of the environs during periods of activity or travel. *Eris* appear to respond to the utility of vantage positions by conducting extensive visual surveys (bouts of turning) from elevated positions in the vegetation. Although the factors which enable *E. marginata* to pursue a steady course

through vegetation have not been analyzed in detail here, it is suggested that they can maintain such a course by the periodic recognition of distinctive features of the surrounding vegetation, during the frequent episodes of visual survey which accompany locomotion.

The response of these small (5-7 mm) spiders to visual stimuli at distances of at least 10 meters is remarkable, as is the almost unerring accuracy of their jumping behavior in three dimensions.

Although *E. marginata* is found in other neighboring habitats at times (such as upon the heavy horizontal bars of chain-link fences in the area), it is most often encountered on the larger blackberry bushes. It is seldom encountered with a sweep net in grassy areas that are far removed from this habitat. Several aspects of the behavior of this species may help to explain this distribution or microhabitat preference. First of all, the horizontal leaves of the blackberry are adjoining and often overlapping at inner angles, thus affording these spiders their typical shelter sites. *Eris* tend to move toward the elevated positions of blackberry bushes relative to other plants in an open field. The bushes grow in open, unshaded, habitats which afford *Eris* the sunshine which they seem to "enjoy." It could be said that the radiation requirements of the blackberry leaf and this jumping spider coincide. The strength of the stems and leaves of the blackberry is more than adequate to support the jumps of this spider, which moves clumsily through grasses. The same plant structure also facilitates the visual activities of *Eris* by providing relatively large vistas and extensive surfaces for movement, including the avenues of large stems. With foot-pads, extraordinary powers of vision for a creature of its size, and a complex repertoire of behavior, *Eris* is well-suited for its role as a little tiger of the blackberry bush.

Among salticids, one might classify *Eris marginata* as a searcher, rather than a pursuer (Enders 1975). Nonetheless one should entertain the possibility that activity patterns in a particular habitat may vary greatly from those observed elsewhere, even for the same species, depending upon relative availability of sedentary and actively moving prey species.

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