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The behavior of *Eris militaris* (Araneae: Salticidae)

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Preface

This version incorporates sketches and photographs from a somewhat informal 1975 study of *Eris militaris* in Corvallis, Oregon. It is hoped that these sketches will add to the original descriptive material (Hill 1978). Since that time, the name previously associated with these common spiders (*Eris marginata*, as described by Peckham and Peckham 1909, and Kaston 1972, 1973) has reverted to *E. militaris* (Hentz 1845, per Maddison 1986). Otherwise, only minor changes have been incorporated into the text of this version.

Introduction

Eris militaris is the most conspicuous of the jumping spiders inhabiting blackberry bushes (*Rubus*) in the vicinity of Corvallis, Oregon. Although the larger salticid *Phidippus johnsoni* (see Edwards 2004) occasionally ventures out upon the lower leaves of a blackberry bush, *E. militaris* is the largest jumping spider to consistently appear in this habitat (Figs. 1-2). Several species of *Pelegrina*, as well as a *Tutelina* which is probably not described (close to *T. similis* in appearance, covered with light blue scales) were also common in blackberry bushes in this area. An undescribed species of *Habronattus*, since named *H. ophrys* by Griswold (1987), was also frequently encountered on open ground under these blackberry bushes.

Fig. 1. Blackberry bush (*Rubus*) in Corvallis, Oregon (1975). The stems and leaves of this plant were inhabited by salticids of at least five genera, notably *Eris* and *Pelegrina*. The most conspicuous species was *E. militaris*, particularly in May when courting males are common.

Fig. 2. The author in the bush at Witham Hill, Corvallis, Oregon, looking for jumping spiders (1975).

The following "ethogram" was distilled from more than 1160 minutes of observation of more than 25 individual *E. militaris* 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. This period of observation encompassed a portion of the early mating season of these annual spiders, when the males were adults and the females penultimates. Thus, while there is 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.

E. militaris is sexually dimorphic and both males and females are easy to identify at a distance (Figs. 3, 4).

Diurnal activity patterns

The life of *E. militaris* was greatly regulated by warmth and sunshine. The spiders generally traveled on the

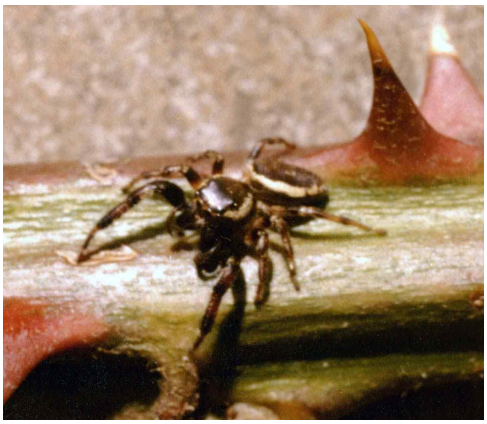

Fig. 3. Adult male *Eris militaris*. Note the long forelegs and broad white lateral bands characteristic of the male of this species.

Fig. 4. Adult female *Eris militaris*. This female was covered with white scales, and the dorsum of the opisthosoma displayed characteristic markings.

upper, illuminated surfaces of blackberry leaves and stems. They often moved into the sunshine when feeding upon prey. In the morning these spiders, emerging from their shelters, flattened themselves along a leaf or stem in a normal orientation to the solar radiation, most probably to increase their body temperature. When *basking* in this manner, the appendages were held close to the body and the spider moved little. The dorso-opisthosomal position of the heart may greatly facilitate the rapid distribution of heat throughout the body of a basking spider. In this regard it is significant that the opisthosoma was pivoted to bring the dorsum to face the sun more directly. *Eris* appeared to be most active in the mid-day heat in Oregon. It was at this time that most active travel and exploration took 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* began to construct and occupy shelters between adjoining blackberry leaves. The spiders remained in these shelters throughout the night, and emerged the next day only if the weather was favorable. As the air cooled in the evening, the spiders were often seen basking as in the morning.

Locomotion

Eris walked slowly about in their shelters in the evening, if they moved at all, and were quite sluggish until they warmed up in the morning (unless threatened). The spiders were only active when the warmth and illumination are favorable, and it was thus that these spiders, particularly the vagabond males, engaged in the greatest amount of travel in the middle of the day. Like other jumping spiders, *Eris* employed at least five basic methods in their movement upon vegetation. Most of the time they were walking at various speeds (or running), with pretarsal foot pads in contact with the surface. They often jumped to a sighted target position. They also descended (*rappelled*) on a dragline, or climbed a vertical dragline. Finally, like many other spiders, they constructed and climbed on the underside of a horizontal bridge of silk, or similarly used a thin plant stem as a bridge.

Eris walked almost equally well on the underside of a leaf or stem as they did on the top, although they used the upper surfaces most often. In addition to their usual forward advance, *Eris* were quite capable of side-stepping and walking backwards at variable speed. They often side-stepped (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 were no real stereotyped sequences. Thus a jump could precede another jump, or a run, or a series of slow turns. The sequence in which each element of the locomotory repertoire was employed was largely determined by the spider's surroundings. If a spider could reach between two leaves, it might continue a walk. If not, it might jump, or turn to reach toward another object. Movement involved continuous visual and tactile evaluation of the immediate possibilities.

The most frequently observed walking pattern may be termed an *exploratory walk*. In this walk the spider took a variable number of steps, then stopped, then took a few more steps, then stopped, and so on. After several intervals of this pattern, the spider might *pause* to survey the environs systematically, pivoting its prosoma to orient the large anterior medial eyes (AME) in various directions. Information received during this pause might lead the spider to alter its course completely. Periodically, during a pause or long stop, the omnipresent dragline, a strand of strong silk continuously released by the moving spider, was secured to the substratum with an adhesive attachment disk. Although the forward walk was characterized by steps, stops, and pauses, the actual pattern was quite variable, as was the speed of the moving spider. A fast moving spider running along a main stem might take many steps between stops, and it might turn quickly to face each of several different directions only briefly during each infrequent pause. A slower spider might 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 might enter a slower, exploratory phase of behavior at any time. Thus a male running along a stem could encounter an object of visual interest, such as a moving insect, and it would subsequently move very slowly with frequent turns to survey the environs. Beyond basic feedback from proprioceptors and contact receptors, complex visual stimuli must be critical determinants of the pattern of locomotion.

The actual stepping pattern consisted of alternating movement of legs RI, RIII, LII, LIV and their contralateral counterparts LI, LIII, RII, RIV (see Land 1972). Pedipalps were often moved up and down, although this activity was not restricted to a period of forward locomotion, but also occurred during each pause. *Anthropomorphically*, one might interpret the *pedipalp flicker* exhibited by many (but not all) salticids to be indicative of the state of general excitation of these animals. The legs I were frequently raised in the air and flexed at the junction of femur and patella as a "gesture."

Infrequently the walk became a relatively slow, but continuous "jerky" (with many brief stops) advance. This pattern of *jerky walk* was as distinctive as it is difficult to describe. Similar behavior has been observed in other salticids, including *Phidippus* and *Platycryptus*. More recent video studies (unpublished) of *Phidippus* have shown that this pattern involves *two* rapid and sequential movements of each leg during each step, compared to only *one* movement of each leg during each step during normal movement. The visual effect is very wasp-like.

The jump of *Eris*, like that of many other salticids (Parry and Brown 1959), depended primarily upon force exerted against the substratum by legs IV. *Eris* jumped clumsily and inaccurately between grass blades which were generally too weak to support this ground force. On blackberry leaves, *Eris* often walked backwards to secure a foothold for a jump. Each jump was preceded by visual examination of the target object with the AME. The spider crouched and flexed legs IV at the tibio-metatarsal joint, and raised legs I and II (flexed at the femur-patella joint) to receive the new surface. Just before each jump, the opisthosoma pivoted to bring the spinnerets into contact with the substratum, and the spider released an adhesive mass of silk to form an attachment disk for its dragline. When a jump was missed, the spider hung by the dragline and was thus able to recover to its former position. A jump involved the exertion of a calculated thrust to project the spider upon a ballistic flight for the required distance, including about 1-20 cm of horizontal flight. In the course of this trajectory the spider rotated as much as 180^0 to receive the new surface, although much of the turning may have actually taken place during the landing itself. *Eris* often jumped up to the underside of a leaf from the top of a lower leaf. Most jumps were unerring in their accuracy, even if made in rapid succession.

While a missed jump could result in a sort of (unintended) dragline descent, at times *Eris* secured an attachment disk and then descended (*rappelled*) on the dragline to a lower position. Spiders could stop at any time during the descent, and would then either continue their descent, or turn to climb the line and recover the original position.

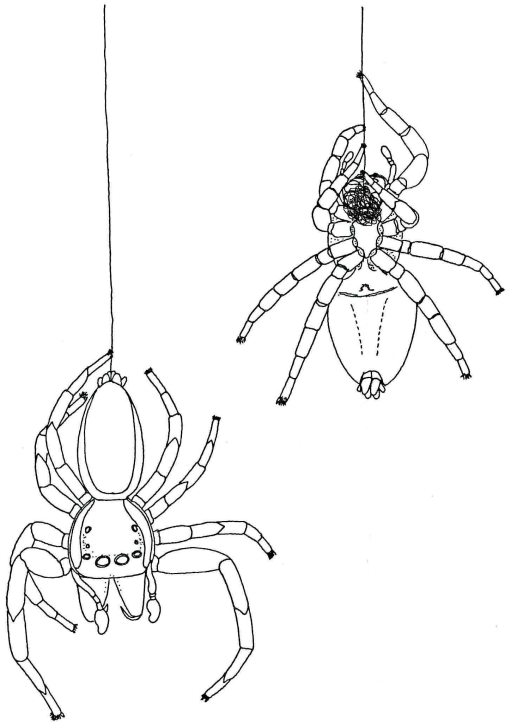

Fig. 5. Vertical descent and ascent with the dragline. The male at left stopped during its descent, holding the line with leg RIV. The female at right was climbing a dragline with the first two pairs of legs, with legs III and IV outstretched (*vertical climbing behavior*).

Eris could ascend either newly-formed or a pre-existing vertical draglines very quickly, utilizing a vertical climbing behavior (observed 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 was wound into a ball that was immediately discarded as the spider attained its objective (Fig. 5).

A very distinctive pattern of travel involved the formation and use of a bridge by *E. militaris* to move between plants. I have observed essentially the same behavior in *Sassacus papenhoei*, but have never seen *Phidippus* construct these bridges (although like many other spiders, they will use them if they are present). Beginning at a vantage position at the end of a stem or at the top of a plant, the spider first descended 5-10 cm on a dragline, then ascended 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 was quite distinctive, as there was virtually no pause between the descent and subsequent ascent of the dragline by the spider. Several strands of silk were then ballooned with the wind, and within a minute or so these were almost invariably attached to an object roughly at the same elevation in the vegetation as the spider. The spider then turned and pulled in the slack on the bridge with legs I, perhaps testing for attachment. Then the spider climbed

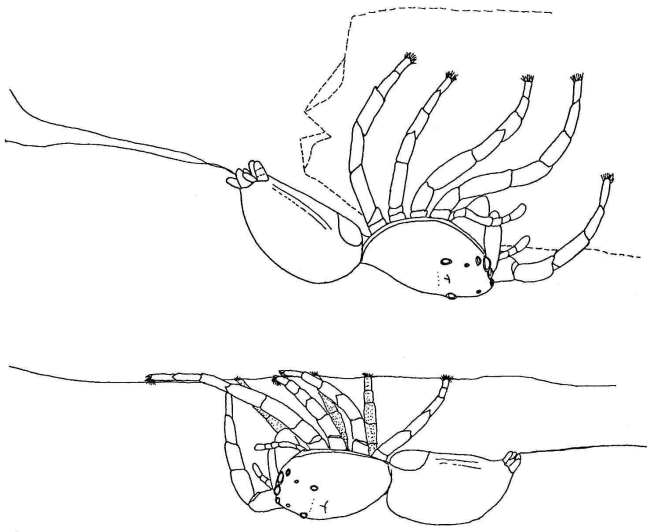

Fig. 6. Bridging. At top an inverted female was ballooning silk with the wind, from the edge of a leaf. Below, the female climbed quickly under the resultant bridge.

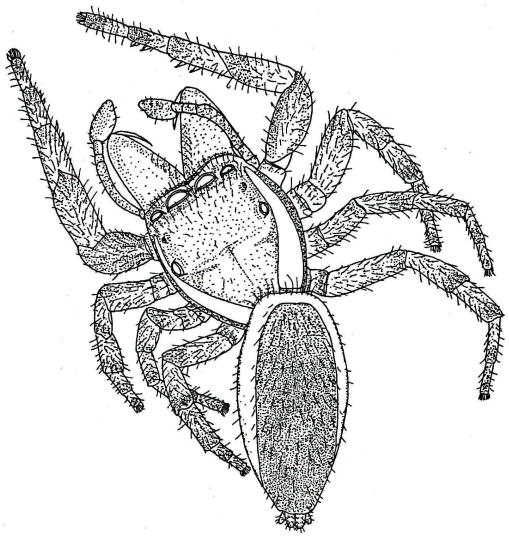

Fig. 7 During an exploratory walk, a male *Eris militaris* turned to watch a butterfly pass three meters overhead.

quickly along the underside of this horizontal bridge, using all legs in what probably corresponded to the normal stepping pattern, to attain its destination (Fig. 6). It is of interest that a brief descent on the dragline invariably preceded the formation of this bridge. It is likely that this behavior was necessary to draw out the initial strands of silk to such a length as might be captured, and subsequently drawn out, by the wind itself. The descent which preceded the formation of a bridge was distinct from the *rappel*, in that the former involved a rapid turn to ascend *without* pause.

Eris could 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 was like that employed by the spider upon a bridge of its own design. It should be noted that bridging behavior (with silk) is used by many non-salticid spiders to facilitate movement upon vegetation.

At times individual *E militaris* appeared to wander greatly, without apparent destination. They often, however, maintained a fairly steady course when moving through vegetation. While maintaining such a course, the animals would periodically stop to survey an elevated (highly visible horizon marker) "objective" plant, then continued their advance. Thus they appeared to travel more or less directly toward a rather distant goal. At times the spiders consistently ascended as they climbed or jumped from leaf to leaf. Often they would survey a position with the AME, and would then employ an indirect route to attain that sighted position, as necessitated by the immediate arrangement of branches and twigs. Visual survey played a primary role in the determination of a course by *Eris*.

Sensory activity

Eris constantly used the front eyes (AME, ALE) to survey the environs during periods of activity, as noted above. During pauses, the spiders would employ a series of small turns of the prosoma to survey the surroundings. They often turned directly toward each of several nearby leaves in succession, suggesting that the lateral (ALE and PLE) eyes were capable of directing movement to face stationary objects. This observation (as well as the role of the ALE in depth perception) challenges the idea that the lateral eyes are used only for movement detection. The AME and ALE were brought to bear upon an object by *facing turns* of the prosoma, which could be pivoted through smaller angles in any direction, without stepping. In addition to lateral movement, the front of the prosoma (*face*) was raised to look up, or lowered to look down. *Eris* turned to face moving objects at distances ranging from several mm to more than 10 m (Fig. 7).

It is well known that the AME of salticids are used 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 were remarkably alert, and the accuracy of each turn to face a stimulus was remarkable. *Eris* would 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* displayed a great deal of tactile sensitivity. The forelegs in particular were often tapped against the surface. In addition the pedipalps were frequently brought to touch the underlying plant. This behavior may facilitate the role of chemosensory as well as mechanosensory setae.

Predation on insects

Eris jumped directly upon sighted prey, generally small insects, which were encountered during a journey through the vegetation. If the prey were detected at a

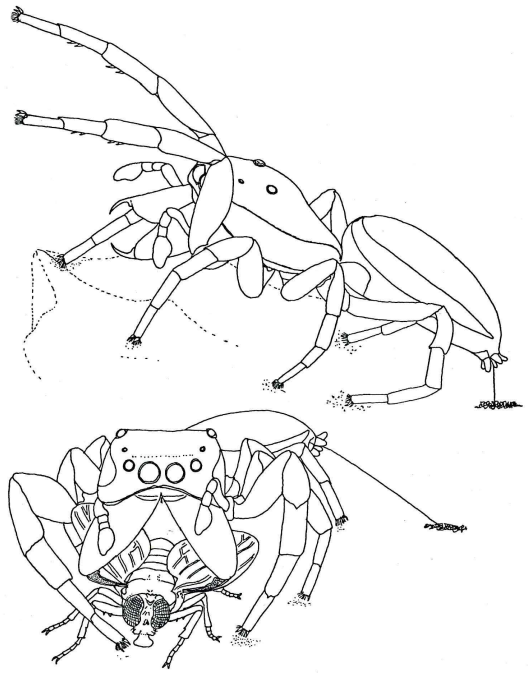

Fig. 8. Predation. At the top a male, having formed an attachment disk, prepared to leap upon prey with forelegs elevated. Below, a male held a captured fly with fangs of the chelicerae.

distance of more than 1-2 cm, the spider would often creep slowly toward the prey with pedipalps flickering up and down, to jump at a distance of 1-2 cm. These spiders would also hurtle themselves into the air at greater distances in pursuit of flying insects. The predatory jump was similar to the locomotory jump, apart from the grasping behavior with chelicerae and legs I and II which were included in the former. The attack was also preceded by formation of an attachment disk (Fig. 8).

When the prey was held securely, after initial maceration or mastication with fangs and chelicerae, *Eris* carried it to a "secure" feeding position. In the evening, spiders would often carry the prey into their shelters to feed. At mid-day, a feeding spider might move into a sunny position with a good view, such as the top of a leaf or stem. When feeding, the spider crouched against the substratum, holding the legs against the body. Fluids were rhythmically pumped into and out of the prey. *Eris* occupied the better part of an hour feeding on a small insect, such as a leafhopper, although the time of feeding on each kind of prey item was quite variable. Subsequently the remnants of the prey were dropped and the spider groomed in place by rubbing the pedipalps in loosely alternate fashion over the front of the chelicerae.

Grooming

The chelicerae were attentively groomed after each feeding, but they were also rubbed against the pedipalps at other times. The pedipalps were on occasion rubbed against each other as well, or used to groom the first leg. The hairy pedipalps were used (like the vertebrate eyelid or nictitating membrane) to brush the AME. The lateral surfaces of the legs and pedipalps were often brushed against the substratum, or against adjacent appendages. The tarsi and pretarsi if the legs were frequently pulled between the endites and chelicerae. This grooming may facilitate the efficient adhesion of these structures, much as the preening of a bird contributes to its ability to fly (Hill 1977). Grooming occurred not only after feeding, but also during a pause in activity. It was commonly seen when the spider was residing in its shelter, or occupying an otherwise concealed position in the vegetation. A spider walking along a stem might pause, turn in several directions, clear the tip of a rear leg between the endites, and then continue its walk.

Non-predatory relations with other species

Eris oriented toward any moving objects within their field of vision, whether these were 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 a nearby wasp, elicited prolonged interest by the spider. *Eris* fled from even small ants, a behavior which may have been related to the fact that these ants would run directly toward the jumping spider (prey is not supposed to do this). *Eris* exhibited no interest in moving ants as prey, nonetheless. By comparison, the much smaller *Tutelina sp.* in this area were observed feeding on the same ants a number of times.

Large vertebrates, such as man, elicited flight and concealment as they approached 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 immobile, however, such large creatures may be observed by the jumping spider for an extended period of time, without flight.

Intra-specific relations

Mature male *E. militaris* responded 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 comprised a sort of courtship dance. This was comparable to the visual display described for other salticids (Crane 1949, Richman 1977). In this dance the male faced the object of its attention, raised and extended its forelegs at a wide angle, held its body well above the substratum, lowered and turned its opisthosoma to the side, and periodically side-stepped in either direction while flexing its extended forelegs rhythmically at each tibio-metatarsal joint (Fig. 9).

Most penultimate females and males immediately fled from this performance, and the courting males pursued them until out of sight. At this point the pursuing male would stop and continue its display while turning to face each of several directions in turn. In a laboratory arena, adult females cannot escape so easily, and this performance is generally a prelude to mating.

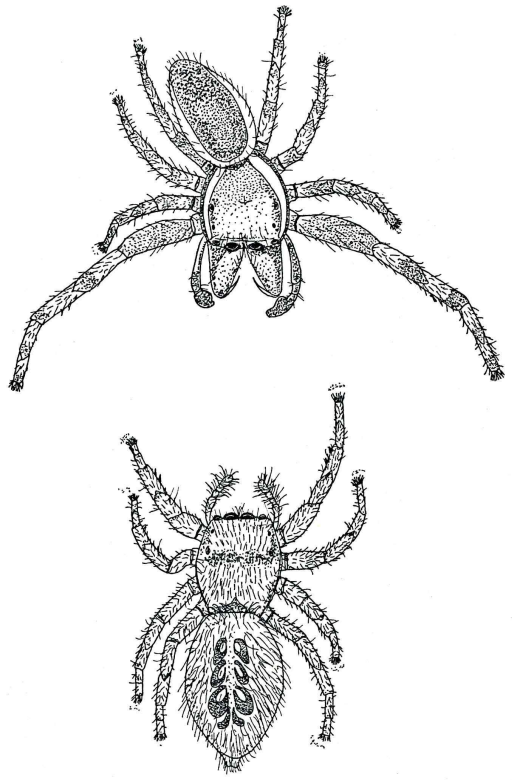

Fig. 9. Courtship. The male, at top, faced the female and extended its long forelegs. The opisthosoma of the male was lowered and turned to the side. The forelegs were raised in a rhythmic gesture, then lowered slowly, as the male stepped slowly from side to side.

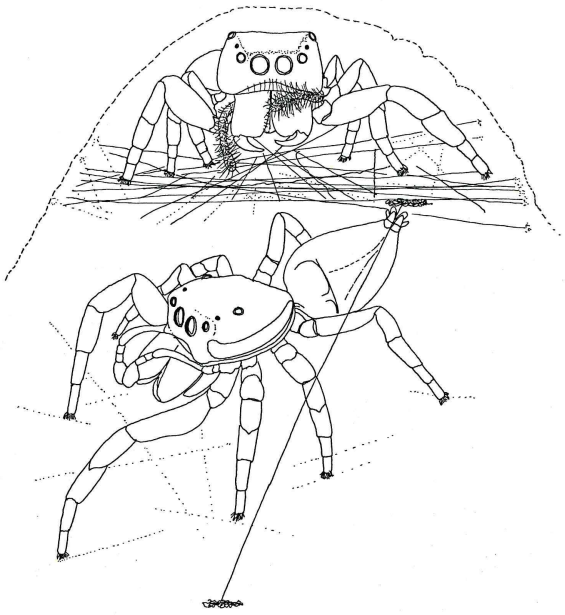

Fig. 10. Cohabitation of male and female. This male (below) was adding silk to the framework of the lower chamber. The female groomed in the sealed upper chamber.

Upon recognition, females and males tended to flee quickly from members of the same sex. When courted by a male, an unwilling female might 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. militaris* and *Phidippus clarus* (found near the top of herbaceous plants in nearby old-field areas), males cohabited with either penultimate or adult females, in the resting sac. The male *E. militaris* often occupied a chamber directly below that occupied by the female (Fig. 10). In this case there was a certain amount of interaction between male and female, including the vibration of the silken floor of the chamber inhabited by the female, which served as a partition between the two spiders. When not aligned below the body of the female, clinging to this silk partition, the male would often vigorously add strands of silk to all parts of the shelter. Except for the sac of the female, which was probably the molting sac used for the final molt, this cohabitation shelter was much like the ordinary shelter used by an *Eris* dwelling upon blackberry bushes.

I later (October, 1977) observed the same kind of cohabitation in a related spider tentatively identified as *Eris flava* (Peckham and Peckham 1888, see Maddison 1986) at Newnan's Lake, Alachua County, Florida. 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* that ventured near the nuptial quarters. In response to the stabs of the forelegs of this small spider, the larger intruder fled. This singular observation shows that the territorial defense of cohabiting males is not restricted to members of the same species in application. John Anderson (University of Florida) also observed four instances of male/female cohabitation for *Phidippus otiosus* (see Edwards 2004) 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 would rest under a leaf in a concealed position. *Eris* displayed a great deal of apparent 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 occupying such a position between two adjoining (overlapping) horizontal leaves or leaflets would attach silk strands between the two leaves, thereby forming a shelter or primitive resting sac (Fig. 11). Thus a shelter might 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) involved the formation of a loose silk platform above the lower leaf. A spider resting on this shelter platform was thus protected from rain water coursing over the lower leaf. During periods of inclement weather *Eris* could

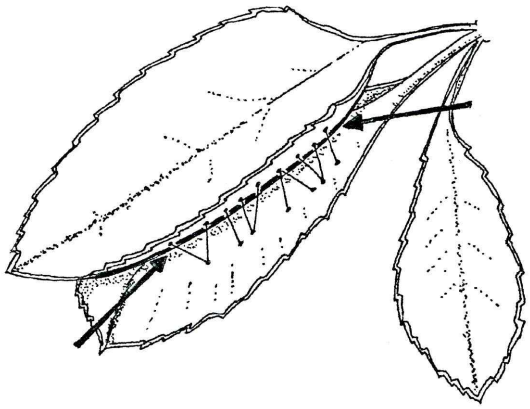

Fig. 11. Diagram showing the attachment of silk between two leaves in the first stage of shelter formation by *Eris militaris*. Arrows indicate the two exits of this shelter. Subsequently a platform may be constructed above the lower leaf.

remain in the shelter, adding to its structure 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 could occupy the top of the shelter, beneath the top leaf and above the horizontal platform. This was most likely utilized as a molting or brooding sac.

The deposition of the individual silken strands which comprised the shelter was often a continuous activity, with stops to attach each strand and on occasion longer pauses or inactive periods. At times the spider would remain at one of the exits, looking out. At other times the spider appeared to be testing tits 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 was raised or lowered and pivoted with great agility, even *grace*. The six spinnerets wove in their fashion like so many small and agile fingers. During the phase of shelter construction *Eris* would still venture out onto nearby leaves to capture prey should the opportunity arise, but would remain in the vicinity of the shelter. Subsequently the spider could move directly back to its shelter, even if its position was visually obscured by leaves. The spider definitely exhibited a memory of the area around its nest.

In favorable weather, with warmth and sunshine, *Eris* emerged to become wandering nomads until late afternoon or evening, when a new shelter would be constructed for the night.

Discussion

The acute vision provided by the AME of these spiders was most often employed in survey of the environs during periods of activity or travel. *Eris* appeared to conduct extensive visual surveys (bouts of turning) from elevated or vantage positions in the vegetation. Although the factors enabling *E. militaris* 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 that accompany their locomotion.

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

Although *E. militaris* was found in other neighboring habitats at times (such as upon the heavy horizontal bars of chain-link fences in the area), it was most often encountered on the larger blackberry bushes. It was seldom encountered with a sweep net in grassy areas that were 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 was more than adequate to support the jumps of this spider, which moved clumsily through grasses. The same plant structure also facilitated 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* was well-suited for its role as a little tiger of the blackberry bush.

Among salticids, one might classify *Eris militaris* 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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