

EPIGAMIC DISPLAY IN JUMPING SPIDERS (ARANEAE, SALTICIDAE) AND ITS USE IN SYSTEMATICS

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ABSTRACT

A study was made of visual epigamic displays in representative species of North American jumping spiders, with a special emphasis on determining the value of using such displays in systematics. Several presumed homologies in courtship behavior were described which largely support the most recent subfamilial arrangement on morphology. Courtship was found to be of more use in some generic and specific level problems, especially with closely related sympatric species. Agonistic displays were found to be of less use in systematics than courtship, because of the similar ways in which males engage in combat display, even in distantly related genera.

INTRODUCTION

The Salticidae (jumping spiders) is the largest of all the spider families, with approximately 3200 described species (Prószyński 1971). These spiders are diurnal vagabond hunters, which visually orient toward prey. They capture prey by jumping on it. Salticids have a characteristic "squared-off" prosoma (or cephalothorax) and are easily recognized by their enlarged anterior median eyes. The family is most diverse in the tropics, although a large fauna occurs in temperate areas. The species exhibit a great variety of form and coloration that has both intrigued and confused the systematists who have tried to work out a reasonable classification within the family. The males are often colorfully ornamented and thus have quite a different appearance than the females, which are usually more cryptic. This male ornamentation appears to function primarily in visual courtship (Peckham and Peckham 1889, 1890, Crane 1949).

Platnick (1971) pointed out that courtship (defined here as intraspecific male-female interactions, which precede and are preparatory to successful mating) is probably the most useful of behaviors for species level systematics because elements of it serve as isolating mechanisms. In the case of jumping spiders, visual courtship, because of the complexity of the displays, is probably more useful than the non-visual (cohabitation) courtship which has been observed in some species, especially of *Phidippus* (Jackson 1976, 1977, 1978). Certain aspects of visual courtship such as the basic patterns of male movements or postures may also be more conservative than some other behaviors, such as cryptic or mimetic behaviors which are more related to environmental change, and may show similarities between closely related groups. Crane (1949) proposed a graded behavioral classification consisting of "runners," "intermediates" and "hoppers." Crane characterized each of these groups by their normal means of locomotion, courtship and

agonistic display (defined here as intraspecific male-male interactions, including those which are similar to courtship and those which involve fighting). This system was not meant to be a natural classification, but a series of evolutionary grades, through which several different genetic lines had passed. As Crane pointed out, under this system many displays may reflect parallelism among the subfamilies. Also the means of locomotion, which is used as a major criterion for the classification, is itself a very plastic adaptation to a specific environment. Crane (1949, text fig. 2) also proposed some courtship characteristics (abdomen twisting, etc.) which might help define subfamilies. It is my contention that such visual courtship behavior can, with caution, be useful for the systematics of taxa ranging from the species level to the subfamilial level. Agonistic displays are less useful because they may not occur in all species and they contain fewer species-specific elements than does courtship. During the last eight years I have gathered observations and films of North American salticid courtships and I am now able to present preliminary findings on the application of visual courtship behavior to some systematic problems in the family Salticidae.

MATERIALS AND METHODS

Adult and immature salticids of 48 North American species are obtained by field collecting in southern Arizona [*Metacyrba californica* (Peckham and Peckham), *Sarinda cutleri* (Richman), *Metaphidippus manni* (Peckham and Peckham), *M. vitis* (Cockerell), *Sassacus papenhoei* Peckham and Peckham, *Pellenes arizonensis* Banks, *P. clypeatus* (Banks), *P. cf. coecatus* (Hentz), *P. hallani* Richman, *P. hirsutus* (Peckham and Peckham) and *P. tarsalis* Banks], Ontario [*Pellenes calcaratus* Banks and *P. viridipes* (Hentz)], Georgia [*Pellenes coecatus* (Hentz) and one male of *Metacyrba undata* (DeGeer)] and Florida (the rest of the species). These were maintained in the laboratory in plastic vials and fed fruit flies (*Drosophila melanogaster* Meig.) or cabbage looper larvae [*Trichoplusia ni* (Hübner)]. Immature specimens were reared to maturity. Apparently healthy individuals of both sexes were placed together in arenas of plexiglass or plastic (including petri dishes) and filmed or observed during their courtship or agonistic display. Most of the courtships were recorded on super-8 color film (high speed Ektachrome®) using Bolex® 280 macrozoom or Beaulieu® 4008 movie cameras. In most cases visual courtships were filmed under artificial light with a film speed of 18 fps (normal speed), but one film was made in natural light and another was shot at twice normal speed. Analysis of the courtships was conducted through a frame-by-frame inspection of each film. Events were timed based on the film speed and ethograms of selected courtships were constructed.

Virgin female salticids were, in general, more receptive to males than previously mated females, but with some species [*Marpissa pikei* (Peckham and Peckham), *Sarinda cutleri* (Richman), *Hentzia mitrata* (Hentz)] only mated females were available. Females of these and of *Pellenes brunneus* Peckham and Peckham (females of which were strongly resistant to mating in the laboratory) were chilled to allow the male to go through the entire display without interruption. In most other cases virgin females were used at room temperature (20-25°C). Generally, the male was introduced to the arena first and the female dropped down on her dragline in front of the male.

Experiments were conducted with three species, one each of Crane's behavioral groups, to determine how important pheromones might be in courtship. Filter paper was placed in petri dishes containing a female spider and left for 24 hrs. This was then cut in half and

placed with a clean half in a clean petri dish. A male of the same species was introduced and a filming speed of 2 fps was used to record the males' actions for three minutes. The last two minutes of these films were used to analyze the male reaction and time spent on each half circle of paper. The technique is a modification of a method used by Hegdekar and Dondale (1969) for lycosid spiders.

RESULTS AND DISCUSSION

A summary of the courtships of 48 species of North American salticids is presented in this section. Some representative courtships are depicted in ethograms (Appendix Figures 1-13). Notes on agonistic displays are incorporated in the text, but as these are not as useful as visual courtship in systematics they will not be discussed in as much detail. The species of salticids are arranged in the subfamilies in which they seem to fit, based both on current morphological studies (Prószyński 1976, Hill 1979) and courtship behavior. The subfamilies proposed by Petrunkevitch (1928, 1939) and utilized by Crane (1949) in her Table II have proven to be an inaccurate reflection of the phylogeny of the various genera in the family. Crane's behavioral classification (R = "runner", I = "intermediate", H = "hopper") as it would apply to each species is presented for comparison. Mountings are recorded in the text only for unchilled virgin females.

Subfamily Lyssomaninae:

Lyssomanes viridis (Walckenaer) (R). Early Movements: stationary for 5 sec at a time, then approached directly, repeat. Later Movements: as in early. Retinae of AME: moved back and forth. Palpi: held 90° to substrate (straight up) stationary. First Legs: extended laterally, tarsi-metatarsi jerked alternately at intervals, prior to forward motion. Prosoma: raised off substrate. Opisthosoma: bent downward. Number of Observations: 2. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: male with elongated and enlarged chelicerae; front legs longer than in female.

Crane (1949) noted the retinal movements of males of *Lyssomanes bradyspilis* Crane during courtship. These eye movements were also noted in *L. viridis* (Walck.), but they have been also observed in relation to prey capture in other salticids (Bristowe 1941, Land 1969). These may thus be simply scanning movements by the retinae of the male, which are accelerated because of the heightened stimulus of the female presence. The unusually transparent prosoma of *Lyssomanes* makes such retinal movements more noticeable than they would be in other salticids. The species of *Lyssomanes*, because of their unique morphology (both in eye position and epigynal and palpal structure) and their distinctive courtship, warrant at least a separate subfamily.

Subfamily Marpissinae:

Marpissa bina (Hentz) (R). Early Movements: direct toward female. Later Movements: zigzag. Palpi: lowered, stationary. First Legs: raised. Prosoma: low to substrate. Opisthosoma: raised. Number of Observations: 1. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: sexes very similar; males usually darker, females with central light band on opisthosoma.

M. pikei (Peckham and Peckham) (R). Early Movements: direct. Later Movements: direct. Palpi: lowered, stationary. First Legs: raised. Prosoma: low or occasionally slightly raised off substrate. Opisthosoma: raised. Number of Observations: 2. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: sexes differ primarily in pattern, males being darker with central dark band on opisthosoma.

M. sulcosa Barnes (R). Early Movements: zigzag. Later Movements: zigzag. Palpi: stationary. First Legs: raised. Prosoma: raised. Opisthosoma: raised, twisted to right or left. Number of Observations: 6. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: sexes very similar.

Maevia inclemens (Walckenaer) (H). Early Movements: zigzag. Later Movements: direct. Palpi: mostly stationary. First Legs: raised, moved back and forth. Prosoma: raised. Opisthosoma: straight. Number of Observations: 5. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: "normal" phase male similar to female, except for having yellow hairs on palpi and stripes and spots on femora of legs; black phase male differs from female in having black body and three tufts above anterior eyes.

This subfamily, as characterized by Prószyński (1976), bears little resemblance to the subfamily of Barnes (1958) and even less to that of Petrunkevitch (1928, 1939). Of the genera examined, I would retain only *Marpissa* and *Maevia*. Males of the genus *Marpissa* tend to exhibit courtships in which the opisthosoma is raised nearly perpendicular to the substrate. One species, *M. sulcosa* Barnes, differs from the others in twisting the opisthosoma to the right or left and exhibiting a zigzag motion with the prosoma elevated. It is the latter motion and elevation of the prosoma which seems to link *M. sulcosa* to *Maevia*. The genera are also similar in several morphological characteristics, such as in having four pairs of spines on the ventral first tibiae. These genera are separated by Prószyński (1976), who restricts the subfamily to the genus *Marpissa* alone.

Subfamily Aelurillinae:

Menemerus bivittatus (Dufour) (R). Early Movements: direct or at slight angle. Later Movements: direct. Palpi: stationary. First Legs: partly raised, occasionally lowered during stationary periods. Prosoma: low. Opisthosoma: straight. Number of Observations: 12. Number of Males: 3. Number of Mountings: 7. Sexual Dimorphism: sexes differ primarily in pattern of dorsal surface, males with dark central stripe on opisthosoma, females with wide light band.

Metacyrba californica (Peckham and Peckham) (R). Early Movements: direct, jerky. Later Movements: direct, jerky. Palpi: stationary. First Legs: raised, vibrated slightly. Prosoma: low. Opisthosoma: straight. Number of Observations: 4. Number of Males: 3. Number of Mountings: 3. Sexual Dimorphism: sexes very similar.

M. undata (DeGeer) (R). Similar to *M. californica* except: Palpi: extended laterally, during early courtship stationary. First Legs: extended laterally during early courtship, raised to position like that of *M. californica* in late courtship, raised and lowered slightly during forward motion. Prosoma: raised. Opisthosoma: bobbed during mounting. Number of Observations: 2. Number of Males: 1. Number of Mountings: 1. Sexual Dimorphism: sexes very similar.

Phlegra fasciata (Hahn) (I?). Early Movements: zigzag. Later Movements: direct. Palpi: not observed. First Legs: not recorded. Prosoma: not recorded, probably low. Opisthosoma: straight. Number of Observations: 1. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: sexes similar, male with cephalic area brighter red than that of female; clypeus turquoise blue.

The genera *Menemerus*, *Metacyrba* and *Phlegra* seem to be related, based on the similarities of their very simple courtships. Hill (1979) has found the opisthosomal scales of the first two genera to be nearly identical and unlike those of *Marpissa*. He has also divided the North American *Metacyrba* into two genera, *Metacybra* [*M. taeniola* (Hentz) and allied species] and *Platycriptus* (*M. undata* and allied species). I am inclined to agree

that this division is probably needed (based on morphology), although I have no data on the courtship of *M. taeniola*.

I doubt whether these genera should be placed in the Aelurillinae, but they do not seem to belong to the Marpissinae, as thought by Petrunkevitch (1928) and Barnes (1958) or the "Habrocestinae" of Hill (1979). *Phelgra* has been placed in the Pelleninae (Petrunkevitch, 1928), but does not seem to belong there based either on courtship or on morphology (Prószyński 1976).

Ethograms of the typical courtships of both *Menemerus bivittatus* and *Metacyrba undata* (Figures 1-2) indicate the relative simplicity of the displays in this group of genera.

During the current study, males of *M. bivittatus* were observed to spend more time on areas of filter paper which had been in contact with virgin females than on clean filter paper (79% of 2-minute times periods on female-contacted paper, $n = 10$, $SD = 1.8\%$, males = 2). This is taken as evidence for the existence of a possible contact pheromone. Other jumping spiders tested [*Hentzia palmarum* (Hentz) and *Pellenes brunneus* Peckham and Peckham] exhibited no preference.

Menemerus bivittatus males were also observed engaged in both ritual agonistic display and fighting. Two males were sighted on the outside of a building in Gainseville, Florida. One male (the larger of the two) approached the other male, which was inside a silk retreat under a wooden beam. The second male eventually came out of its retreat after the first male started a side-stepping display. Both displayed with the first legs widely spread and nearly parallel to those of the other male. They fought, using their chelicerae at close range. At intervals they broke away from one another and the larger male finally drove the smaller male away, briefly occupying the abandoned silk retreat. It should be noted that Bhattacharya (1936) reported agonistic display for this species in India. Crane (1949) stated that *M. bivittatus* had no agonistic display.

Subfamily Synemosyninae:

Sarinda cutleri (Richman) (R). Early Movements: direct. Later Movements: with some indication of zigzag. Palpi: extended laterally, stationary. First Legs: raised, vibrated. Prosoma: raised. Opisthosoma: not observed. Number of Observations: 2. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: Male with scale-covered elongated chelicerae.

S. hentzi (Banks) (R). Early Movements: zigzag. Later Movements: direct? Palpi: extended laterally, stationary. First Legs: raised, wave in unison. Prosoma: raised. Opisthosoma: bobbed up and down. Number of Observations: 5. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: male with scale-covered elongated chelicerae.

Synemosyna formica Hentz (R). Early Movements: not observed. Later Movements: direct. Palpi: not observed. First Legs: raised. Prosoma: raised. Opisthosoma: bobbed up and down. Number of Observations: 1. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: sexes very similar.

The ant-mimicking salticids were all placed into the Synemosyninae by Prószyński (1976), but several objections can be raised about this treatment. The members of *Sarinda* and *Synemosyna* raise their first legs in courtship, whereas the members of the genera *Synageles*, *Semorina* and *Peckhamia* (see Crane 1949, Table II) have a quite different courtship approach, the first legs being lowered and the opisthosoma being raised vertically or moved from side to side. The genital morphology seems also to

separate these groups and to relate the former two genera with *Myrmarachne*. It thus is quite doubtful that ant mimicry arose only once as Prószyński would seem to indicate.

Subfamily Sitticinae:

Neon nelli Peckham and Peckham (I?). Early Movements: zigzag. Later Movements: zigzag. Palpi: raised and lowered in unison. First Legs: raised, moved in unison. Prosoma: only slightly raised. Opisthosoma: straight. Number of Observations: 2. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: sexes very similar.

Sitticus cursor Barrows (I?). Early Movements: direct. Later Movements: zigzag. Palpi: not observed. First Legs: first raised then lowered. Prosoma: only slight raised. Opisthosoma: straight. Number of Observations: 5. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: sexes very similar, male slightly darker than female.

There may be some difficulty with the placement of *Sitticus* and *Neon* in the Sitticinae (Prószyński 1976), but not enough is known about their relationship at present to settle the matter.

Subfamily Thiodininae:

Thiodina puerpera (Hentz) (I?). Early Movements: not well observed. Later Movements: not well observed. Palpi: lowered, stationary. First Legs: raised. Prosoma: raised. Opisthosoma: lowered. Number of Observations: 1. Number of Males: 1. Number of Mountings: 1 (mated with female *T. sylvana*). Sexual Dimorphism: sexes differ primarily in dorsal color pattern, male generally darker than female and with dark or banded legs.

T. sylvana (Hentz) (I?). Early Movements: lateral or direct, very slow, jerky. Later Movements: not observed. Palpi: lowered, mostly stationary. First Legs: raised, then raised and lowered alternately or in unison, no apparent pattern. Prosoma: raised. Opisthosoma: lowered. Number of Observations: 2. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: dimorphism as in *T. puerpera*, from which this species differs in details of dorsal pattern.

While I am inclined to agree with Prószyński (1976) that *Thiodina* is closely related to the Dendryphantinae, I have kept its separation from the latter subfamily based on the unusual sensory hairs on the first pair of legs and differences in body scales (Hill 1979). However, based on the structure of the palpi and epigyna and on the courtship behavior it should be closely allied with the dendryphantines.

Subfamily Dendryphantinae:

Eris marginata (Walckenaer) (I). Early Movements: zigzag. Later Movements: zigzag? Palpi: lowered, stationary. First Legs: raised, jerked. Prosoma: low to slightly raised. Opisthosoma: lowered. Number of Observations: 2. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: male with somewhat elongated and enlarged chelicerae, usually darker with more contrasting markings than female, dorsal markings different.

Hentzia grenada (Peckham and Peckham) (I). Early Movements: often zigzag, sometimes straight. Later Movements: as in early. Palpi: extended laterally. First Legs: extended laterally, raised, lowered alternately and in unison several times. Prosoma: raised. Opisthosoma: twisted to right or left, straightened at intervals. Number of Observations: 25. Number of Males: 2. Number of Mountings: 6 (matings only with virgin female *H. palmarum*). Sexual Dimorphism: male with elongated chelicerae, body more elongate than female, clypeus of male white and first legs dark, dorsal markings different.

H. mitrata (Hentz) (I). Courtship as in *H. grenada* except front legs raised and lowered more often, usually with each forward movement. Number of Observations: 9. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: male with fringe of white hair on first legs, first legs more elongate, dorsal markings different.

H. palmarum (Hentz) (I). As in *H. grenada*. Almost impossible to distinguish the two species on the basis of courtship. Can hybridize with *H. grenada*. Number of Observations: 31. Number of Males: 11. Number of Mountings: 10. Sexual Dimorphism: dimorphism essentially as in *H. grenada*, from which this species differs in details of dorsal pattern.

Metaphidippus galathea (Walckenaer) (I). Early Movements: zigzag. Later Movements: zigzag. Palpi: moved with no pattern. First Legs: lowered, bent upward slightly. Prosoma: low. Opisthosoma: straight. Number of Observations: 3. Number of Males: 2. Number of Mountings: 1. Sexual Dimorphism: sexes differ in color pattern, males with more distinct markings and with white scales and hairs on darker background color.

M. manni (Peckham and Peckham) (I). Early Movements: zigzag. Later Movements: zigzag. Palpi: extended laterally, raised and lowered in unison while moving. First Legs: lowered extended laterally at wide angle at first, narrowing as male approaches female. Jerked at intervals. Prosoma: low or only slightly raised. Opisthosoma: straight. Number of Observations: 3. Number of Males: 3. Number of Mountings: 1. Sexual Dimorphism: sexes differ in color pattern, male with more distinct markings and with white stripes on clypeus and chelicerae.

M. sexmaculatus (Banks) (I). Early Movements: direct. Later Movements: direct. Palpi: moved with no pattern. First Legs: raised, moved with no pattern. Prosoma: Low. Opisthosoma: straight. Number of Observations: 2. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: sexes very similar.

M. vitis (Cockerell) (I). Early Movements: zigzag, with some arc-like motion. Later Movements: as in early. Palpi: stationary. First Legs: raised, crossed, jerked at intervals. Prosoma: low. Opisthosoma: straight. Number of Observations: 3. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: sexes very similar, males darker in color.

Phidippus pulcherrimus Keyserling (I). Early Movements: zigzag. Later Movements: direct. Palpi: stationary. First Legs: raised, jerked. Prosoma: raised. Opisthosoma: straight. Number of Observations: 1. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: male with black and white fringes on first legs; opisthosomal markings more distinct; palpi with contrasting white and black areas.

Sassacus papenhoei Peckham and Peckham (I). Early Movements: zigzag or spiral. Later Movements: as in early. Palpi: not observed. First Legs: raised, crossed, raised and lowered later during lateral movements. Prosoma: low. Opisthosoma: straight. Number of Observations: 1. Number of Males: 1. Number of Mountings: 1. Sexual Dimorphism: sexes similar.

Tutelina elegans (Hentz) (I?). Early Movements: zigzag. Later Movements: zigzag. Palpi: extended laterally, stationary. First Legs: raised, waved alternately or in unison (erratic). Prosoma: raised. Opisthosoma: straight. Number of Observations: 4. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: sexes differ in color, males with grey scales on body, black fringe around eyes and with white tarsi on first legs, female iridescent green on dorsal surface.

The genera in the Dendryphantinae are, in some ways, difficult to characterize. While the subfamily is distinct morphologically, it is behaviorally polythetic—no one courtship characteristic being common to all, or even most, genera. Yet, most of the genera are

related to one or more genera within the subfamily by one or more behavioral traits. For example, opisthosomal twisting is common in some genera (*Hentzia*, *Zygoballus*, and some *Phidippus*) and one of these, *Phidippus*, is linked to *Eris*, *Tutelina*, and even *Thiodina* by its characteristic side-stepping hesitating movement, with first legs raised and prosoma elevated.

The similarity of the courtships of *Sassacus papenhoei* and *Metaphidippus vitis* may indicate that these two species are congeneric, both belonging to *Sassacus* as proposed by Hill (1979). Males of both species raise and cross the first legs, lower the prosoma, jerk the first legs up and down at the start of their sideways runs and both have zigzag or spiral paths to the female. *Zygoballus*, although not studied in the current work, has both a similar morphology and similar epigamic displays to the dendryphantines (Peckham and Peckham 1889). I thus agree with Hill (1979) that the Zygoballinae of Petrunkevitch (1928) should become part of the Dendryphantinae. In morphology *Zygoballus* resembles *Eris* while in courtship and agonistic display it resembles *Hentzia*.

The genus *Hentzia* is an example of a group of species which exhibits ecological separation, possible competitive exclusion, and apparent recent contact between closely related species. *Hentzia palmarum* (Hentz) seems to have been a long time resident in Florida, whereas *H. grenada* Peckham and Peckham may have relatively recently invaded Florida from the South America-West Indies area. The latter is primarily found on palms, especially the saw palmetto in the north. It has been collected as far north as the Okefenokee Swamp in Georgia, but is more abundant in the slash pine-palmetto areas of south Florida. *H. palmarum* has been collected in abundance on coastal mangroves, willow trees along lakes, *Lyonia* and scrub oaks in sand pine scrub and turkey oak-longleaf pine associations, and on various other shrubs. It is very rarely collected on palms, although it may be collected next to *H. grenada* in mixed palmetto and shrub understories. The two species have nearly identical courtship (Figures 3-5) and agonistic displays and will interbreed in the laboratory; virgin females of *H. palmarum* readily accepted males of *H. grenada*. In interspecific agonistic display-fights between equal sized males, the male of *H. grenada* always won. The resultant progeny of crosses between *H. palmarum* and *H. grenada* never matured ($n = 2$), but the sample is not large enough for any conclusions. Morphologically the two species are distinct, although they are closely related enough to be quite similar. Males of *H. grenada* appear to lack the variation in cheliceral length which has been observed in males of *H. palmarum*. All of the males of *H. grenada* collected in Florida and Georgia (approximately 20) had very long chelicerae, longer than for a male of *H. palmarum* of similar size.

The courtship of both species is relatively complex, although in a few cases a male approached a female and mated with her after very little visual display. At the start of most of the displays the male was facing the female at a distance of 3-4 cm. Usually any movement of the female initiated a display by the male. He would then spread his first legs widely apart (approximately 100°) and advance toward the female, usually with the opisthosoma twisted to the right or left and raised approximately 30° . Most males proceeded in a zigzag path toward the female, with pauses about twice a second, during which the opisthosoma was straightened and then twisted again. A few males (Figure 4) switched the opisthosoma from right to the left or left to right during the display, but most kept one orientation or the other when the opisthosoma was twisted. The magnitude of the zigzags varied from a nearly straight path to sideways motions of as much as 1 cm. When the male was within 1 cm of the female he usually straightened his abdomen and extended his first legs forward, toward the female. During the final stage of

courtship the male alternately raised and lowered his first legs two or three times, in addition to raising them slightly at the start of each forward movement. If the female was receptive (which she usually was, if virgin—of 12 virgin *H. palmarum* females, 10 accepted males) the male moved forward, alternately touching one first leg to the female and then the other in a see-saw manner approximately five times. He then mounted and twisted the female's opisthosoma around so that he was able to insert one of his palps into one side of the epigynum, later repeating with the other palpus on the other side. Males often shifted from one side to the other several times, until the female started moving and apparently disengaged herself. Males removed from a female after mounting usually resumed copulation without repeating courtship.

Both *H. palmarum* and *H. grenada* were observed to perform identical agonistic displays which often ended in fighting. The displays, which were observed eight times for *H. palmarum* and nine times for *H. grenada* (not counting interspecies displays) began with one or both males extending the chelicerae, raising the first legs slightly, and raising and twisting the opisthosoma. Both males moved forward and began a rocking motion in synchrony; the first legs were extended laterally and eventually were parallel to those of the other male. The fangs were extended and the males fought (this usually occurred even if the males were not evenly matched). Finally one broke away and ran. The displays were very short, usually lasting less than 15 seconds.

Subfamily Euophryinae:

Corythalia canosa (Walckenaer) (H). Early Movements: usually direct. Later Movements: zigzag. Palpi: rotated, one clockwise, other counter-clockwise in phase. First Legs: lowered, raised slightly during motion. Prosoma: raised. Opisthosoma: straight. Number of Observations: 11. Number of Males: 5. Number of Mountings: 1. Sexual Dimorphism: sexes similar, male with white scales on clypeus and chelicerae, palpi more contrastingly marked than those of female.

Habrocestum bufiodes Chamberlin and Ivie (H). Early Movements: body moved back and forth by shifting position over legs, some zigzag motion. Later Movements: as in early. Palpi: raised and lowered alternately or in unison. First Legs: lowered. Prosoma: raised. Opisthosoma: straight. Number of Observations: 4. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: sexes differ in color pattern, males with more contrastingly marked palpi; markings more distinct than those of female.

H. pulex (Hentz) (H). Early Movements: zigzag or arc. body tilted toward direction of movements. Later Movements: zigzag or arc. Palpi: lowered, stationary, occasionally raised and lowered slightly in unison or while body tilted, one lowered and one raised. First Legs: lowered during early courtship; raised during later courtship. Prosoma: lowered early, raised later. Opisthosoma: straight. Note: female actively participates in display, usually causing male to move in arc or circle around her. Number of Observations: 2. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: sexes very similar, males with somewhat more distinct pattern.

H. n. sp. A (H). Early Movements: stationary periods, followed by rapid decreasing arc-zigzag run. Later Movements: as in early? Palpi: raised and lowered alternately or in unison. First Legs: lowered. Prosoma: slightly raised. Opisthosoma: straight. Number of Observations: 10. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: Sexes differ in color pattern, males with bright red cephalic area and with more distinct dorsal pattern.

Neonella vinnula Gertsch (R). Early Movements: whole body vibrated. Later Movements: jumped at female (may be atypical). Palpi: stationary during vibration of body. First Legs: lowered. Prosoma: raised at least slightly. Opisthosoma: straight. Number of Observations: 3. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: sexes very similar.

The genera examined in the current study (*Corythalia*, *Habrocestum* and *Neonella*) seem to be related by their courtship. This relationship is especially evident between some species of *Corythalia* and *Habrocestum*. Prószyński (1976) has placed all three genera into the Euophryinae and has presented convincing evidence of the relationship of these with each other and with *Euophrys*, based on genital morphology. Despite the differences in the opisthosomal scales found by Hill (1979) between *Habrocestum* and *Corythalia*, I find other morphological as well as behavioral evidence to favor Prószyński's classification. I thus do not consider that Hill's "Habrocestinae" is a valid subfamily.

Two of the species of *Habrocestum* are closely related. These are *H. bufoides* and an undescribed species from the Florida scrub and pine forests. These species are very similar, superficially. The genitalia are distinct and their courtships are even more so (Figures 6-7). Males of *H. bufoides* perform a relatively slow rocking display, whereas males of *H. n. sp.* move in rapid arcing runs, the palpi being raised alternately at the end of each run. The motion is so fast that slow motion at one-half normal speed was needed so that the movies could be analyzed. The species are also somewhat ecologically isolated, although they were occasionally found together in ecotones. *H. bufoides* was abundant in mesic hammocks and pine flatwoods in north Florida, whereas *H. n. sp.* was collected in turkey oak-longleaf pine and sand pine scrub associations. The full description of the new species will be presented in a planned revision of *Habrocestum*. None of the species of *Habrocestum* was observed to exhibit any kind of agonistic display.

Courtship in *Corythalia canosa* (Walckenaer) (Figure 8) is similar to that of *C. fulgipedia* (Crane 1948:28) in that the male's first legs are kept down on the substrate and the palpi are rotated in a clockwise-counter clockwise fashion (the left palpus was observed in one example to be moving clockwise, while the right palpus moved counter-clockwise). The male courtship usually began approximately 3 cm from the female. The first legs of the male were extended laterally and the palpi were in constant motion at the rate of 3.33 turns per second. The path of the male showed considerable variation, being zigzag to nearly direct. The male moved forward in jerky motions, with his body somewhat elevated off the substrate and the opisthosoma straight. Females usually responded to the approach of the male by raising the first legs and elevating the prosoma (also seen in *Habrocestum pulex* and some *Pellenes*). All females observed either exhibited this behavior or ran from the male. At this point, with the female approximately 1 cm away, the male usually zigzagged back and forth, with his palpi in motion, his first three pairs of legs extended laterally and nearly parallel to each other, and his body elevated. The male then attempted to mount, raising his first legs upward and elevating his prosoma higher. One male finally managed to mount over the female's elevated prosoma, and successfully mated, inserting his emboli alternately into the female's epigynum.

C. canosa differed from Crane's (1948) South American species in that the agonistic displays of males often led to fighting if the males were of similar size. The agonistic display began with a male elevating its prosoma. The opisthosoma was either straight or bent downward and the first three pairs of legs were nearly parallel to each other and were touching the substrate. Either both males approached one another or one initiated

the approach. As in courtship the palpi were in motion most of the time, the movements being mostly up and down, rather than in circles. The approach of the male was jerky, with very short pauses after forward runs. One male was observed to raise his third pair of legs off the substrate while he was under attack. Before contact was finally made in the encounters observed, one or both of the males raised his first legs. Usually one male raised his first legs and the other followed, but this was not dependent on which individual initiated the display. If one of the males had not been driven off at this point, contact was made and the first legs of both males were lowered and held parallel to those of the opponent (similar to the fighting poses of *Menemerus* and *Hentzia*). They fought, pushing each other back and forth and seeming to bite with their chelicerae. One of the males eventually broke away and ran. No fighting took place in one confrontation between males observed in nature. The smaller of the two males retreated after displaying for only a few seconds. Males of *C. canosa* often differed markedly in size. It is doubtful that fights often take place between smaller and larger males as the smaller usually retreated in observed laboratory encounters as well. A total of 30 interactions between five marked males were observed in the laboratory to determine if the same males succeeded in driving away their opponents. In all cases the larger males defeated smaller males, usually without fighting. Males of nearly the same size as their rival fought until one eventually defeated the other. Repeated fights between such males always resulted in the same male "winning." These encounters were observed over three days.

Neonella, while having some morphological and behavioral similarities to the euophryines, may actually belong with *Neon* in the Sitticinae. I have too little data at present to be sure of its placement.

Subfamily Pelleninae:

Pellenes agilis (Banks) (H). Early Movements: zigzag. Later Movements: direct. Palpi: stationary. First Legs: bowed downward, then raised. Prosoma: slightly raised. Opisthosoma: bobbed up and down. Number of Observations: 3. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: male with long fringes on first legs, dorsal color pattern differs from that of female.

P. arizonensis Banks (H). Early Movements: zigzag. Later Movements: direct. Palpi: lowered, some movement in unison. First Legs: bowed downward, then extended laterally and later forward, touching female. Prosoma: slightly raised to low. Opisthosoma: raised slightly, bobbed. Number of Observations: 11. Number of Males: 7. Number of Mountings: 1. Sexual Dimorphism: dimorphism essentially as in *P. agilis*, from which this species differs in details of dorsal pattern.

P. brunneus Peckham and Peckham (H). Early Movements: zigzag. Later Movements: stationary for long periods of time, may arc around female. Palpi: move back and forth, raised and lowered in unison early, later extended forward. First Legs: raised, tarsi jerked at intervals. Third Legs: raised and lowered. Prosoma: low. Opisthosoma: straight, bobbed slightly. Number of Observations: 32. Number of Males: 3. Number of Mountings: 0. Sexual Dimorphism: male with two prominent spatulate spines on prolatateral surface of each first leg, third legs modified with projection on each patella and knobby distal end to femora; latter with dark spots and stripes; dorsal color pattern differs from that of female, male darker.

P. calcaratus Banks (H). Early Movements: direct. Later Movements: direct. Palpi: touch substrate alternately during part of sequence with first legs bent downward, otherwise stationary. First Legs: raised at start of sequence, bends legs downward at tibia-metatarsus joint and vibrates them slowly upward, legs suddenly straightened, then

vibrated slowly downward and quickly raised ca. 6 times—sequence repeated. Third Legs: raised, lowered at intervals. Prosoma: low, lowered further during lowering of first legs. Opisthosoma: straight. Number of Observations: 3. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: males with greenish first legs with white fringes and spatulate spines; third legs modified with spike on each patella; dorsal color pattern differs from that of female.

P. carolinensis Peckham and Peckham (H). Early Movements: direct. Later Movements: direct. Palpi: lowered, stationary. First Legs: raised, waved in unison at intervals. Prosoma: raised slightly. Opisthosoma: bobbed up and down. Number of Observations: 8. Number of Males: 4. Number of Mountings: 0. Sexual Dimorphism: sexes differ in dorsal color pattern, males with more distinct pattern, usually darker.

P. clypeatus (Banks) (H). Early Movements: somewhat zigzag, disorganized. Later Movements: as in early. Palpi: lowered. First Legs: raised, then raised and lowered in unison. Prosoma: lowered. Opisthosoma: straight. Number of Observations: 1. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: male with spatulate spines on first legs: stripes on clypeus; dorsal pattern differs from that of female, male darker.

P. coecatus (Hentz) (H). As in *P. brunneus*. Almost identical. Number of observations: 7. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: male with long greenish fringes and spatulate spines on first legs; third legs modified with projection on each patella; clypeus red; white spots on chelicerae; white areas lateral to clypeus.

P. cf. coecatus (H). Courtship similar to *P. brunneus*, except that the palpi are lowered and mostly stationary. Number of Observations: 17. Number of Males: 11. Number of Mountings: 1. Sexual Dimorphism: similar to that of *P. coecatus* but male with different shaped projections on third patellae; no white spots on chelicerae; no white lateral to clypeus.

P. hallani Richman (H). Early Movements: zigzag. Later Movements: zigzag, in both early and later stages makes short, explosive jumps laterally or forward the width of the body at each of lateral movements. Palpi: lowered, mostly stationary or raised and lowered slightly in unison. First Legs: raised, occasionally raised and lowered in unison. Second Legs: displayed by bending backwards, exposing iridescent femora. Prosoma: low. Opisthosoma: straight. Number of Observations: 10. Number of Males: 3. Number of Mountings 1. Sexual Dimorphism: male covered with iridescent scales; clypeus iridescent pearl; femora of first two pairs of legs flattened or concave anteriorly and iridescent; dorsal color pattern more distinct than in female.

P. hirsutus (Peckham and Peckham) (H). Early Movements: zigzag. Later Movements: not observed. Palpi: not observed. First Legs: raised, lowered alternately. Prosoma: not recorded. Opisthosoma: raised. Number of Observations: 5. Number of Males: 3. Number of Mountings: 0. Sexual Dimorphism: male with long black fringes and iridescent blue metatarsi on laterally flattened first legs; prosoma often with reddish or golden cephalic area; body covered with iridescent metallic scales; much darker in color than female.

P. tarsalis Banks (H). Early Movements: zigzag. Later Movements: zigzag. Palpi: move back and forth in unison, then alternately, then held forward. First Legs: raised and bowed, tarsi jerked. Prosoma: low. Opisthosoma: straight. Number of Observations: 9. Number of Males: 6. Number of Mountings: 5. Sexual Dimorphism: male with longer front legs than female; tarsi of first legs black; palpi black and white; dorsal pattern of male differs from that of female; male darker.

P. trimaculatus (Bryant) (H). Early Movements: zigzag. Later Movements: zigzag. Palpi: extended, moved alternately or in unison. First Legs: raised. Prosoma: low.

Opisthosoma: straight. Number of Observations: 12. Number of Males: 4. Number of Mountings: 0. Sexual Dimorphism: sexes similar except that male has different cephalic markings (white stripes in eye region) than female (dark bands on clypeus); male color pattern more distinct.

P. viridipes (Hentz) (H). Early Movements: direct. Later movements: direct. Palpi: touch substrate nearly in unison as first legs are lowered, otherwise stationary. First Legs: raised, then slowly lowered while being vibrated back and forth and bending downward and inward at the tibia-metatarsus joint, suddenly jerked upward, sequence repeated. Third Legs: raised, lowered at intervals, not correlated to other movements, may be alternate or in unison. Prosoma: low. Opisthosoma: straight, bobbed at intervals. Number of Observations: 3. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: male with greenish first legs with long white fringes and spatulate spines; third legs modified with triangular patellae; male dorsal color pattern differs from that of female; dorsal color pattern very similar to that of *P. calcaratus*.

P. cf. viridipes (H). Early Movements: not well observed. Later Movements: not observed. Palpi: lowered, stationary. First Legs: raised. Prosoma: low. Opisthosoma: straight. Number of Observations: 1. Number of Males: 1. Number of Mountings: 0. Sexual Dimorphism: dimorphism similar to that of *P. viridipes*, but third legs of male not modified.

P. n. sp. A (H). Early Movements: direct. Later Movements: direct, almost motionless for long periods. Palpi: not observed. First Legs: raised. Prosoma: low. Opisthosoma: straight. Number of Observations: 2. Number of Males: 2. Number of Mountings: 0. Sexual Dimorphism: male with long golden-yellow fringes on first legs; clypeus bright red; dorsal color pattern more distinct than that of female.

Pellenes, while morphologically distinct, is such a diverse genus with respect to courtship that it is difficult to characterize. It seems best to retain the Pelleninae for this genus while noting the difficulties involved. Courtships among members of a particular species group were similar (see Griswold 1976). Thus members of, e.g., the *agilis* group (*P. agilis*, *P. arizonensis* and possibly *P. hirsutus*) have similar courtships to fellow species-group members, but differed markedly from other species. Although they are distinct morphologically, the members of the *viridipes* group (*P. calcaratus*, *P. viridipes* and *P. cf. viridipes*) had courtships somewhat similar to those of the members of the *coecatus* group (*P. brunneus*, *P. coecatus* and *P. cf. coecatus*). The one member of the *americanus* group for which courtship was observed, *P. tarsalis*, had a completely distinct courtship from the other species studied, which involved the bowing of the first legs and jerking of the tarsi. *P. hallani*, which is a member of the *umatillus* group, also differed from all other species in that the male jumped its own width at the end of each zigzag, displaying its iridescent first and second femora.

Pellenes is another genus where courtship may be useful to distinguish between closely related species. This is especially true for separating *P. calcaratus* from *P. viridipes* and *P. coecatus* from *P. cf. coecatus*. The latter appears to be a very abundant, but overlooked, undescribed species from the western United States. It has been confused with *P. signatus* (Banks) and more recently with *P. coecatus*.

Ethograms are shown for the courtship of individual males of *P. calcaratus* and *P. viridipes* (Figures 9-10), and *P. brunneus*, *P. coecatus* and *P. cf. coecatus* (Figures 11-13).

In the courtship of *P. calcaratus* (Figure 9) the first legs were bent at the tibia-metatarsus joint and vibrated slowly upward at the start, followed by a sudden straightening of the legs and then a series of approximately eight slow lowerings of the rapidly

vibrating first legs. At the end of each lowering the first legs were suddenly raised again. The palpi were moved only during the early raising of the vibrating and bent first legs. The palpi were raised and lowered alternately at a rate of 1.25/second for 4 seconds. In the courtship of *P. viridipes* (Figures 10) the male's first legs were bent at the tibia-metatarsus joint, both downward and inward. The legs were never raised while so bent, nor were they lowered at a steady rate. Instead they were at times almost stationary in height while the tarsi were rotated in a small circle. The first legs were finally lowered the rest of the way and suddenly straightened and raised. This sequence was repeated. During the initial movements of the first legs the palpi were moved up and down rapidly nearly in unison at a rate of approximately 2.7/second for 1.5 seconds. The third legs of both species were moved up and down and back and forth at intervals, apparently with little pattern. The movements of the first legs and the palpi serve to separate these remarkably similar species (the dorsal patterns of the males are nearly identical). A female of *P. calcaratus* was used to obtain courtship from *P. viridipes* males because no *P. viridipes* females were available. It is unlikely that the male varies the basic movements of the courtship, even in such an artificial situation. The courtship observed for *P. viridipes* matches a published account by Peckham and Peckham (1890). No distinctive agonistic display was observed.

The courtship of *Pellenes brunneus* (Figure 11) usually began when the male was approximately 3 cm from the female. The male initially raised his first legs and spread laterally his palpi as widely as possible. He usually moved in a zigzag during early courtship, switching later to an arc around the female. During early courtship the palpi were raised and lowered at a rate of approximately 3/second for 5-10 seconds, while still being kept widely separated. The male moved forward toward the female while raising and lowering his first legs and pausing several times until he was approximately 0.5 cm from the female. The male then assumed a characteristic pose of members of the *Pellenes coecatus* species groups, with the first legs held high, the palpi lowered, extended forward and held parallel and stationary, and the body low to the substrate. The third legs were pressed to the sides of the opisthosoma. During this pose the male often remained stationary for 15-30 minutes, especially if the female was not turned toward him. If the female turned toward the male, he raised and lowered his first tarsi very rapidly several times and this activity was often preceded or followed by the raising of the third legs, which were also moved backward and forward. The third legs were usually raised one at a time and the male ended the sequence by touching both third patellae together over his dorsal surface and then lowering them to their original positions. Only one mounting was observed and this was with a chilled female. In this case the male continued his display for several minutes, creeping slowly forward until he was able to touch the female. The male then leaned forward and touched the female with one of his first legs several times. This activity was repeated alternately with the right and left legs. The third legs were moved again several times, the last time just before mounting. The male then mounted and attempted to mate as in other salticids.

Virgin females of *P. brunneus* were difficult to obtain and all females seemed to be quite resistant to male advances. This seemed to be true with most other species of *Pellenes* and it is possible that they required conditions which were not present in the laboratory.

The display of *P. coecatus* (Figure 12) was very similar to that of *P. brunneus*, within variation shown by that species, but differed from *P. cf. coecatus* (Figure 13) in that the palpi of the eastern form (*P. coecatus*) were extended laterally and moved up and down during early courtship, whereas the western form (*P. cf. coecatus*) males kept their palpi

lowered and relatively stationary. The eastern form males differed from those of the western form also in coloration, the chelicerae having white patches, the areas lateral to the clypeus being white and the dorsal pattern also being somewhat different.

Only one species of *Pellenes* was observed to have an agonistic display and this was *P. carolinensis* Peckham and Peckham [= *P. tachypodus* (Chamberlin and Ivie)]. The display was quite similar to courtship, except that the males pushed each other back and forth. This display was observed on three occasions in the laboratory.

Subfamily Plexippinae:

Plexippus paykulli (Audouin) (H). Early Movements: zigzag. Later Movements: direct. Palpi: not observed. First Legs: raised. Prosoma: raised. Opisthosoma: straight. Number of Observations: 3. Number of Males: 3. Number of Mountings: 0. Sexual Dimorphism: male with longer first legs than female; clypeus striped black and white; dorsal color pattern more distinct than that of the female.

Plexippus has a rather simple courtship. It is certainly not related to the rapidly moving *Corythalia* as suggested by Crane (1949). The subfamily Plexippinae is retained for this genus mainly because it does not seem to fit elsewhere. The subfamily may be much more important in the Old World.

CONCLUSION

Courtship behavior in salticids can, with reservations, be utilized for systematic work. This can be at the species, genus or subfamily level, although the latter should be approached with the most caution. The separation of closely related species in *Habrocestum* and *Pellenes* are examples of the first. The courtship similarities between species, such as in the genera *Hentzia* and *Corythalia* can help define genera, as an example of the second. Finally the similarities and differences between genera can help to define subfamilies, such as the Euophryinae and the Dendryphantinae. Courtship behavior should be utilized primarily as supporting evidence for classifications or taxon determinations based on morphology, especially on reproductive structures.

Many difficulties lie in determining just which characters, both morphological and behavioral, are synapomorphic (shared derived) and which are symplesiomorphic (shared ancestral). The similar courtships found in the Euophryinae and in members of genera such as *Hentzia* are possible examples of the first and certain widely scattered courtship characters such as the raising of the prosoma may be examples of the second. I believe that with care distinctions can be made, but a thorough knowledge of the species involved must be obtained before these can be reasonably certain.

The adaptive radiation of the salticids has left the systematist with a complex pattern of parallel and convergent evolution. Unfortunately, there is little fossil evidence to help interpret this pattern. Thus it can only be worked out through indirect evidence, including the use of courtship behavior and morphology. The older subfamilial classifications have become, for the most part, unworkable. Future classification systems will not be based on carapace shapes, eye positions and retromarginal teeth, which are often adaptations to a specific environment, but on reproductive morphology, behavior and ecology.

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KEY FOR SYMBOLS USED
IN FIGURES 1-13

- | | | |
|---|--|---|
| <p>Direction of path (DR)</p> <ul style="list-style-type: none"> Path direct Path zigzag Path an arc Movement forward Movement backward Stationary Break <p>Chelicerae (CH)</p> <ul style="list-style-type: none"> Chelicerae in normal resting position Chelicerae extended, fangs not exposed <p>Palpi (PA)</p> <ul style="list-style-type: none"> Palpi raised at angle Right palpus raised Left palpus raised Palpi lowered at angle Palpi extended laterally Palpi extended forward at angle Palpi extended directly forward Palpi moved up and down in unison Palpi moved up and down alternately Palpi moved in circular path, one clockwise, other counterclockwise <p>First legs (FL)</p> <ul style="list-style-type: none"> First legs raised at angle Right first leg raised | <ul style="list-style-type: none"> Left first leg raised First legs lowered at angle First legs held perpendicular to substrate First legs extended laterally First legs extended forward at angle Left first leg raised, both extended forward at angle First legs extended directly forward First legs moved up and down in unison First legs moved up and down alternately First legs vibrated upward First legs vibrated downward First legs slightly curved downward and forward First legs bowed inward First legs bent at tibia-metatarsus joint First legs jerked suddenly upward (straightened) Tarsi and metatarsi of first legs jerked up and down Tarsi of first legs rotated in circle while legs are lowered | <p>Second legs (SL)</p> <ul style="list-style-type: none"> Second legs extended forward <p>Third legs (TL)</p> <ul style="list-style-type: none"> Third legs raised in unison Third legs lowered in unison Right third leg raised Left third leg raised Left third leg lowered <p>Second and third pairs of legs (ST)</p> <ul style="list-style-type: none"> Second and third legs nearly parallel <p>Prosoma (PR)</p> <ul style="list-style-type: none"> Prosoma raised Prosoma moderately raised Prosoma lowered Prosoma tilted to right Prosoma tilted to left <p>Opisthosoma (OP)</p> <ul style="list-style-type: none"> Opisthosoma straight (normal posture in most species) Opisthosoma raised and twisted to right Opisthosoma raised and twisted to left Opisthosoma lowered Opisthosoma bobbed Mounting |
|---|--|---|

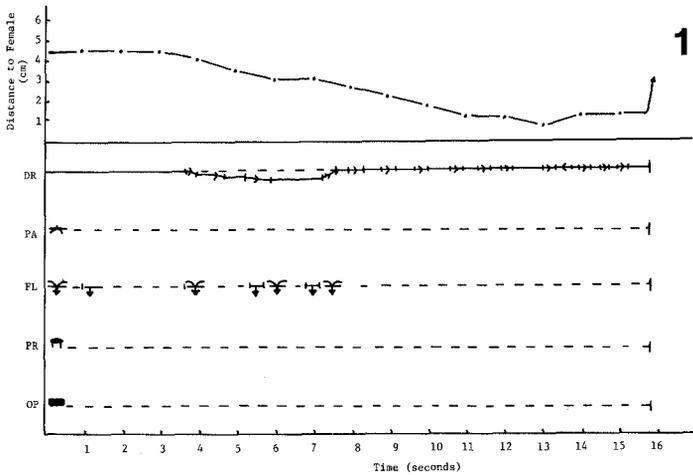


Fig. 1.—Ethogram of courtship of *Menemerus bivittatus* male from Gainesville, Alachua County, Florida.

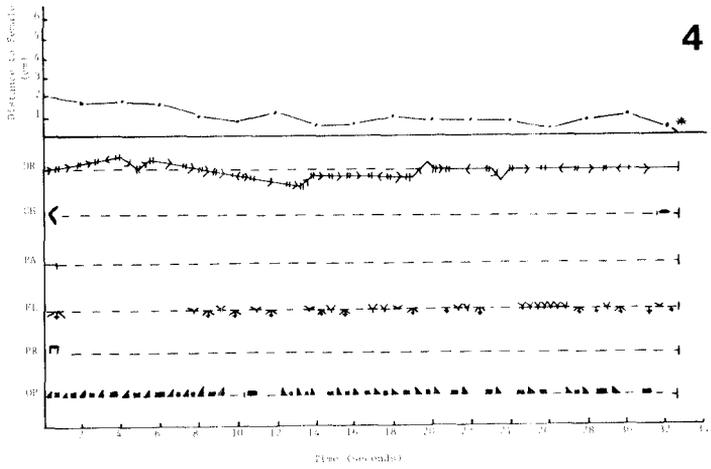
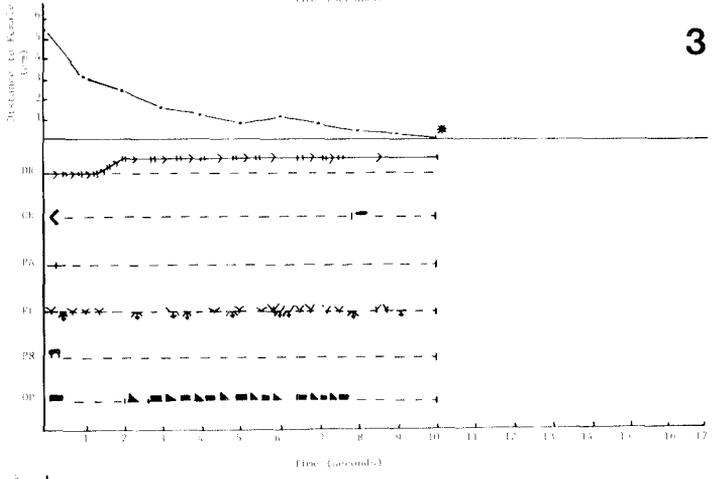
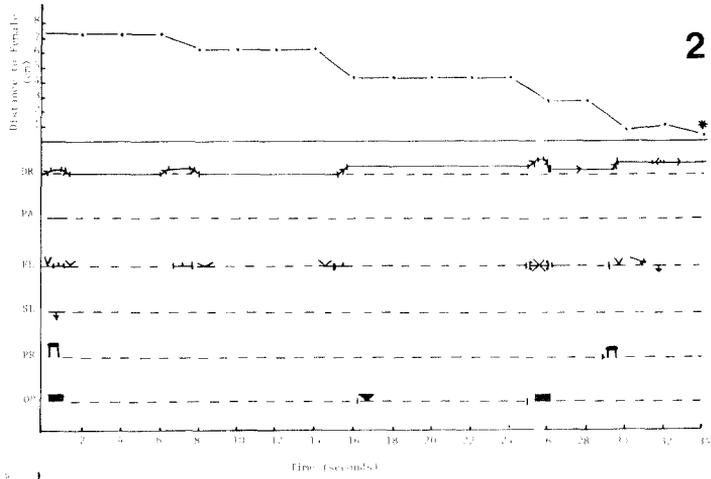
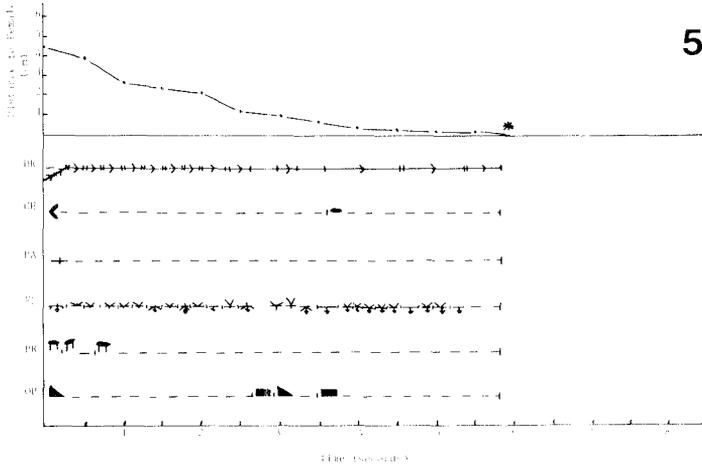
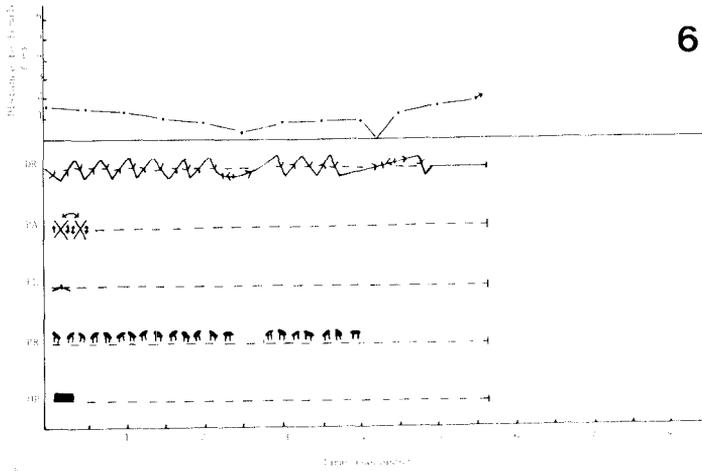


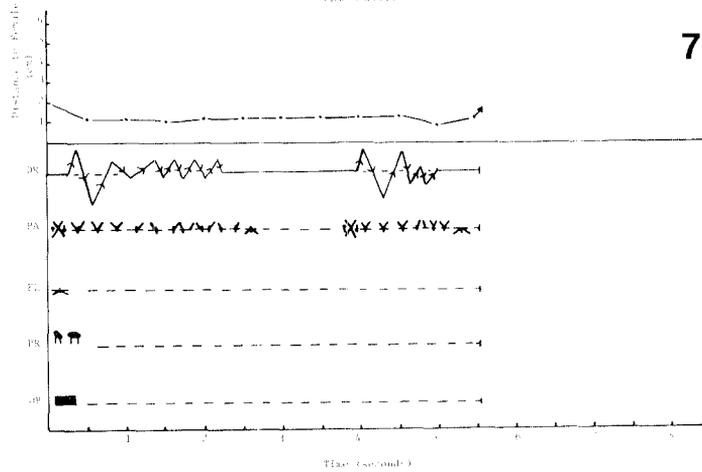
FIG. 2. Ethogram of courtship of *Melanobreda uniseta* male from Charlton County, Georgia.
 FIGS. 3-4. Ethograms of courtship of two different *Bostata palmiana* males from Santa Fe, Low County, Florida.



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Fig. 5. Ethogram of courtship of *Hentzia greeni* male from Archbold Biological Research Station, Volusia County, Florida. Female chilled.
 Fig. 6. Ethogram of courtship of *Haplocephalus hyaloides* male from Lake Ocala, Putnam County, Florida.
 Fig. 7. Ethogram of courtship of *Haplocephalus maculipes* male from Gainesville, Alachua County, Florida.

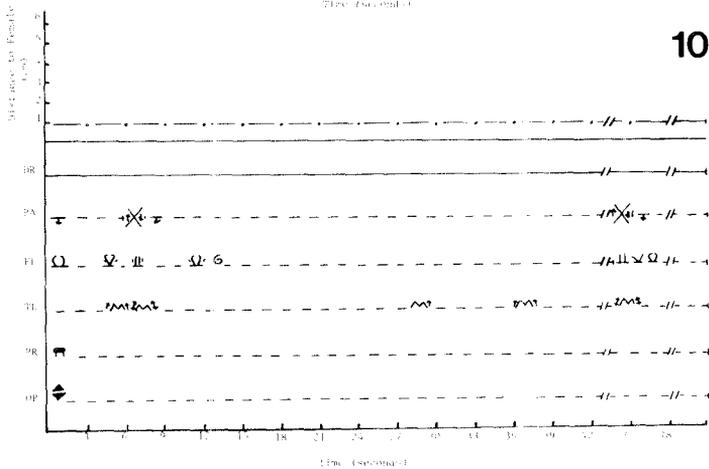
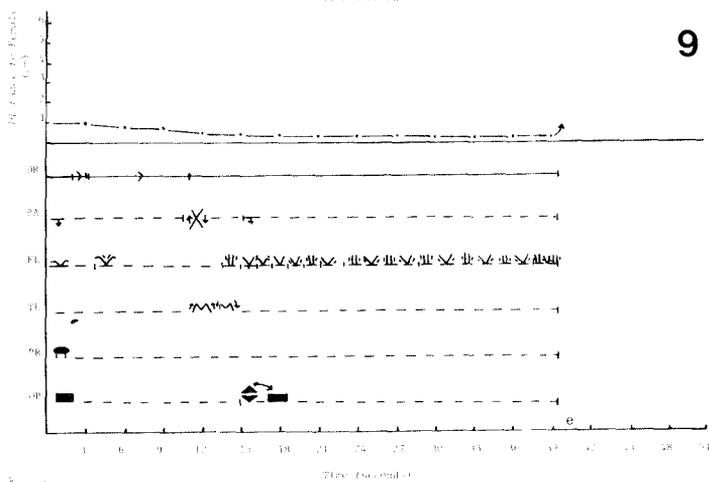
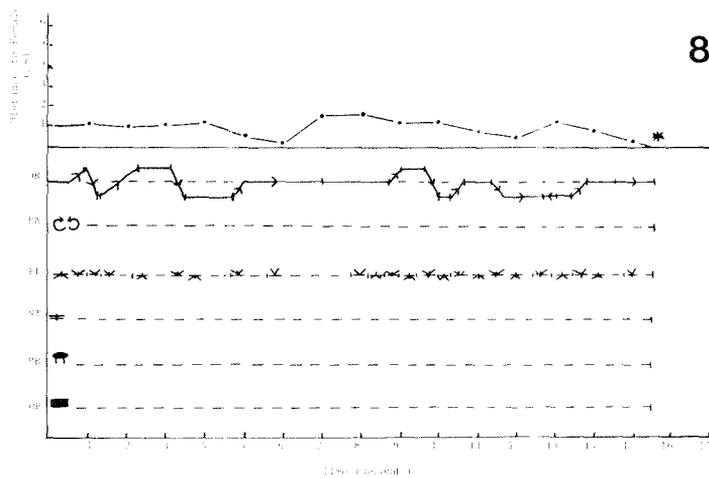


Fig. 8. Ethogram of courtship of *Soryghalva ornata* male from the River Strev, Alachua County, Florida.
 Fig. 9. Ethogram of courtship of *Bellonea calcaratus* male from the Muskoka District, Ontario, Canada.
 Fig. 10. Ethogram of courtship of *Bellonea viridipes* male from the Muskoka District, Ontario, Canada.

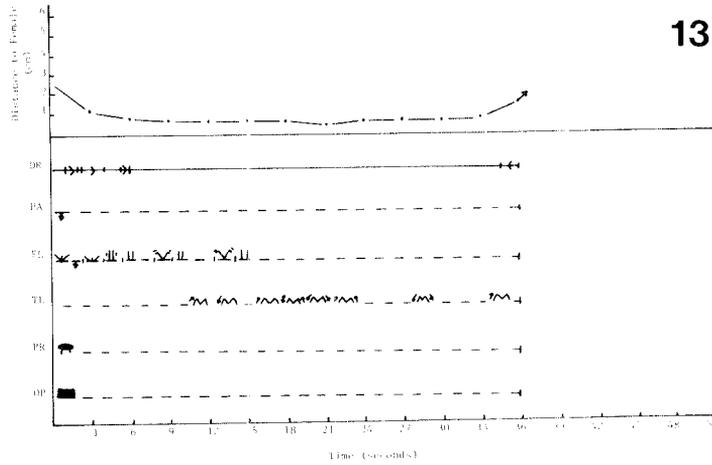
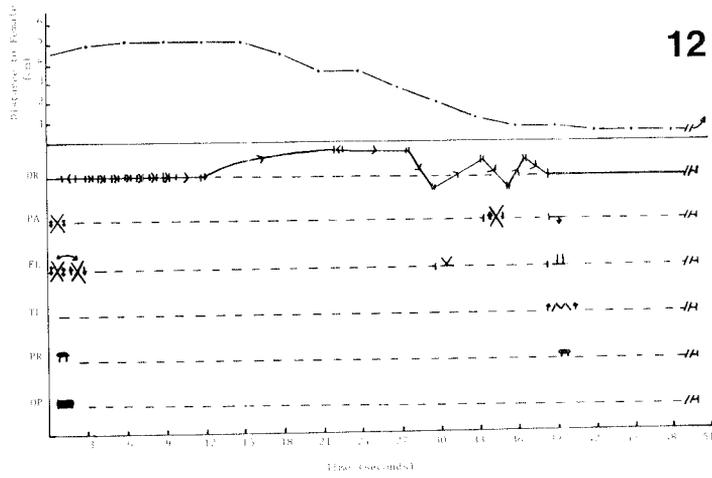
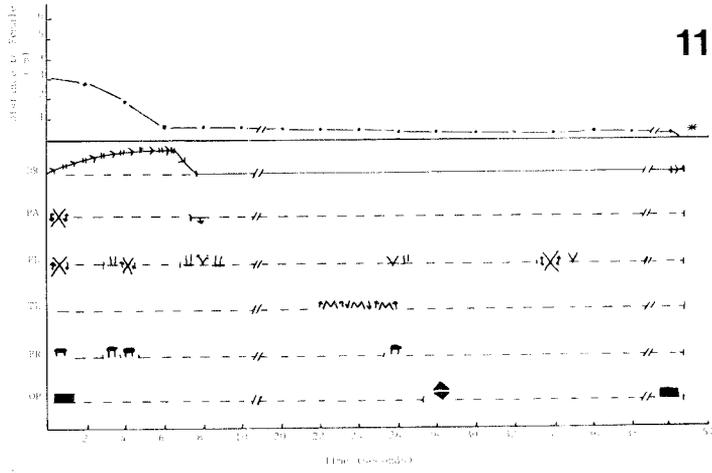


Fig. 11.—Ethogram of courtship of *Palanista browniae* male from Gulf Coast of Levy County, Florida; female chilled.
 Fig. 12.—Ethogram of courtship of *Palanista covatae* male from Jekyll Island, Glynn County, Georgia.
 Fig. 13.—Ethogram of courtship of *Palanista cf. covatae* male from Yuna, Yuna County, Arizona.