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Cover illustration: Scanning electron microscope photograph of the abdomen of a mature female *Philoponella vicina* (Uloboridae). Photograph by Flory Pereira and William G. Eberhard.

PHILOPONELLA REPUBLICANA (ARANEAE, ULOBORIDAE) AS A COMMENSAL IN THE WEBS OF OTHER SPIDERS

Ann L. Rypstra and **Greta J. Binford**[1]: Department of Zoology, Miami University, 1601 Peck Blvd., Hamilton, Ohio 45011 USA

ABSTRACT. Juvenile individuals of the spider species, *Philoponella republicana*, were common in the webs of the social spider, *Anelosimus eximius*, and the solitary spider, *Architis* sp., in the forest habitats of the SE Peru. The abundance, size and location of *P. republicana* individuals were surveyed in each host web. Although the host webs were similar in size and conformation, more *P. republicana* individuals were found in the social spider webs than in the solitary host webs. Likewise, the number of *P. republicana* in the social spider webs was correlated with host web size. The mean size of prey captured by *P. republicana* was 2.1 mm, which was significantly smaller than the prey taken by the social spider, and, in feeding trials, *Architis* sp. individuals reacted only infrequently to prey of that size. This separation in the size of prey taken caused us to conclude that *P. republicana* acted as a commensal for the most part; however, they were observed to prey on the social spiders occasionally. Small *P. republicana* were the most common in both host webs and tended to be high in the barrier webbing. The largest individuals in the social host webs were located under the sheet area, and these individuals were observed to feed more frequently than spiders in other size classes and in other areas of the host webs. We conclude that juvenile *P. republicana* are commensals in both host webs but that they benefit more from the greater amount of activity in webs of the social spiders.

Mounting evidence from phylogenetically diverse species shows that grouping behavior may simultaneously reduce individual risk of predation and enhance feeding efficiency (Pulliam & Caraco 1984; Uetz 1988; Uetz & Heiber 1994). Heterospecific interactions within social groups can bring advantages to individuals in those groups that do not accrue to individuals in single species aggregations (Morse 1970; Barnard & Thompson 1985). Slightly different foraging modes and food preferences may lead to more efficient resource usage by mixed species groups which can simultaneously take advantage of other kinds of advantages of being in a group.

A wide variety of heterospecific relationships have been reported among spider species ranging from predation (Larcher & Wise 1985; Jackson & Whitehouse 1986; Jackson 1990) to kleptoparasitism (Vollrath 1987; Cangialosi 1990), to commensalism (Rypstra 1979; Bradoo 1986, 1989). In many of these instances, host spiders have large complex webs that can provide a living space with some support and protection for the second spider species (Rypstra 1979; Bradoo 1986, 1989; Hodge & Uetz 1992). In particular, the webs of communal or social spiders tend to provide habitat for other spider species who in-

teract with the host in both positive and negative ways (Rypstra 1979; Bradoo 1989; Cangialosi 1991; Hodge & Uetz 1992).

A commensal association occurs when one species reaps some benefits by association with a host species but the host species is essentially unaffected, positively or negatively, by the association. Commensalism has been reported with some frequency among spider species in the family Uloboridae (Struhsaker 1969; Opell 1979; Bradoo 1986; 1989). Bradoo (1989) concludes that *Uloborus ferokus* Bradoo (Araneae, Uloboridae), living in the webs of the social spider *Stegodyphus sarasinorum* Karsch (Araneae, Erisidae), receives protection, support and increased prey capture which increases its lifespan and fitness. The spider species, *Philoponella republicana* (Simon) (Araneae, Uloboridae), is frequently found in single species aggregations (Smith 1985; Binford & Rypstra 1992); but, in addition, we have found immature individuals of the species in the interstices of the webs of almost all complex, semi-permanent spider webs at our study area in SE Peru. *P. republicana* were particularly common in the webs of *Anelosimus eximius* Simon (Araneae, Theridiidae), a cooperatively social species in this area. The goal of this

[1]Present address: Dept. of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA

study is to describe the abundance and distribution of *P. republicana* in the large webs of this social spider in comparison with its distribution in the webs of a solitary species, *Architis* sp. (Araneae, Pisauridae), whose web is of similar size and structure (Nentwig 1985).

METHODS

Data were collected on spider populations inhabiting the subtropical moist forest of the Tambopata Reserved Zone, 35 km southwest of Puerto Maldonado in Madre de Dios, Peru. Data were collected in the dry season: July and early August of 1987, 1988 and 1989 (see Erwin 1985 for complete description of the habitats).

The webs of both host spiders were very similar in overall appearance. They consisted of a dense sheet of webbing subtended by a maze of barrier webbing encompassing neighboring vegetation (Brach 1975; Christenson 1984; Nentwig 1985). *A. eximius* is a cooperatively social species so each web contained several hundred to several thousand individuals that worked together to capture prey (Brach 1975; Christenson 1984). *Architis* sp. is a solitary spider and a single individual monitors insects arriving in the web from a funnel-shaped retreat at one end of the sheet area of the web (Nentwig 1985). Adults of *A. eximius* are 4–6 mm in length, which is substantially smaller than *Architis* adults which are 8–12 mm in length.

Surveys were conducted of all *A. eximius* webs found, a total of 46 webs, between 4 July and 4 August in 1987 (18 webs), 1988 (16 webs) and 1989 (12 webs). To avoid the confounding factor of repeated measures only one survey per social spider web was included in the data set. In order to standardize for season and temperature across the years we selected the first survey conducted on a web after 4 July on a dry day on which the temperature was between 24–28 °C. A total of 12 *Architis* sp. webs were surveyed a single time and under similar weather circumstances in July of 1989. During each survey, *P. republicana* were classified into three size categories: large (4–6 mm in length), medium (2–4 mm in length), and small (less than 2 mm in length). *P. republicana* were also categorized by position in the host web. That categorization included spiders located under the sheet, just above the sheet (within 2 cm), in the low barrier of the web (2–20 cm above the sheet) and in the high barrier (20 cm or more above the sheet).

In order to obtain one measure of site quality

within the host web, we also attempted to determine the feeding frequency of *P. republicana* spiders located in different positions. A spherical bundle in the chelicerae of the spider was evidence that it had captured a prey item recently. One complication that arises in determining the likelihood of feeding is that the spider will feed longer on large prey than on small prey so a survey sampling technique would have biased the results toward large prey. In the case of *A. eximius* webs, we typically spent two or more hours observing so, for this study, we only counted the prey items that were captured during our observation times. For *Architis* webs, we surveyed a second time 2–3 hours after the first observation to estimate a feeding rate in a similar fashion.

To determine whether the two species were actively competing for prey that entered the web or if there was a division of resources based on prey size, we needed to determine the range of prey sizes taken by each of the host species. The distribution and frequency of prey capture were obtained for *A. eximius* in the course of a simultaneous study (Rypstra 1990; Rypstra & Tirey 1991). In order to determine whether the solitary *Architis* sp. actively preys on insects in the size class that *P. republicana* handles, we conducted a feeding experiment. Field-caught fruit flies (*Drosophila* spp. 1.5–2.0 mm in length, the mean size of prey taken by *P. republicana*) were gently blown into each of ten webs of *Architis*. In all cases the *Architis* individual was at the opening of its retreat in a feeding position at the time the prey were introduced. If the *Architis* spider retreated before the prey was in the web or if it was apparent that we had disturbed her in the process, no data were taken. If we successfully introduced the fly without disturbing the host spider and we were able to detect that the fly contacted the sheet in a way sufficient to vibrate the threads, we recorded the reactions of the *Architis*. Between 8–12 flies were tested in each of ten *Architis* webs. After each trial, a larger fly or grasshopper was introduced into the web to see if the host spider was receptive to any prey. If we could not get the spider to respond, the results of the trial were excluded from the analysis.

RESULTS

All of the webs that we found in all three years had some *P. republicana* in them. On average, there were 8.4 ±3.3 (mean ± standard deviation)
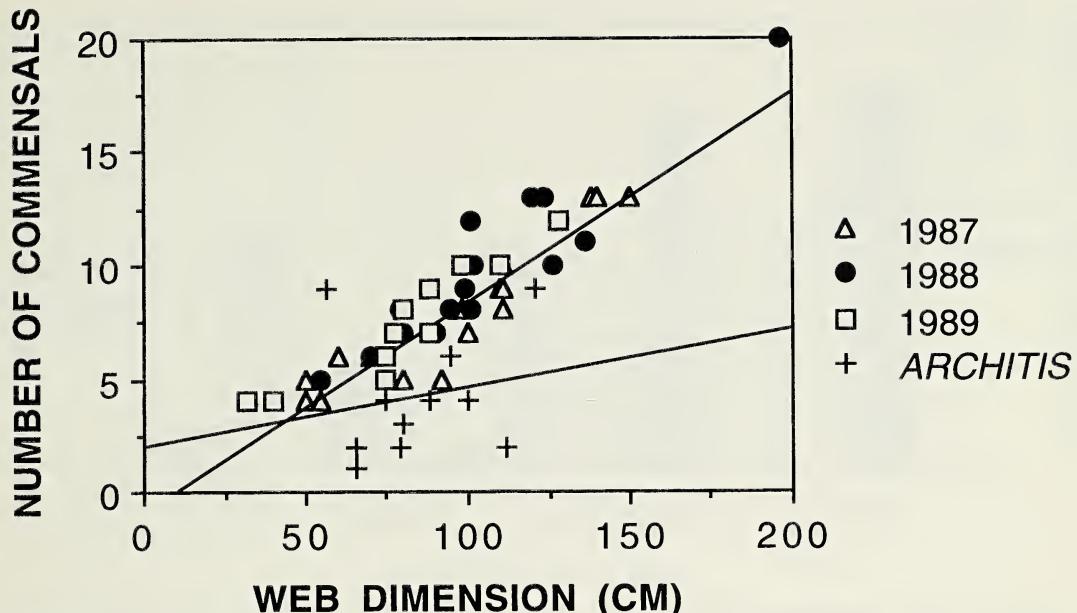
Figure 1.—The number of commensal *Philoponella republicana* individuals *vs.* the longest horizontal dimension of the host web. Data points indicated for the three years (1987, 1988, and 1989) are all for the social host, *Anelosimus eximius*. Data for the solitary host, *Architis* sp., were all gathered in 1989. The correlation between web size and number of commensals is significant for the social *Anelosimus eximius* but is not significant for the solitary *Architis* sp.

P. republicana individuals in the 46 *A. eximius* webs we surveyed over three years. There were no differences among the years (Kruskal-Wallis Multiple Comparisons, $P > 0.05$). There were significant positive relationships between social spider web size and the number of *P. republicana* in the web both within each year and when the data for all years were pooled. The strongest relationship was between the longest horizontal dimension and number of spiders (for all years together: Spearman's $r = 0.85$, $P < 0.05$) (Fig. 1).

We found a mean of 4.17 ± 2.6 *P. republicana* individuals in the 12 webs of *Architis* sp. that we surveyed in 1989. This was significantly less than the numbers we found in the social spider webs (Mann-Whitney *U*-Test, $P < 0.05$). The webs of *Architis* and *A. eximius* were similar in all the dimensions we measured: longest horizontal, perpendicular or web height, and height of the sheet above ground (Mann-Whitney *U*-Test for all, $P > 0.25$). However, there was no relationship between web size and number of *P. republicana* individuals in *Architis* sp. webs (longest horizontal web dimension and spider number: $r = 0.4$, $P > 0.2$) (Fig. 1).

The distribution of *P. republicana* individuals in the various size classes we identified was not even within either host web (χ^2 Test, $P < 0.05$). In both web types, small spiders were most abundant and large spiders the least abundant (Fig. 2). The size distributions of *P. republicana* in the two host types were significantly different from one another (χ^2 Test, $P < 0.05$). Most noticeably, there were more large individuals in *A. eximius* webs than there were in the webs of *Architis* sp. (Fig. 2). The distribution of *P. republicana* webs across the four positions we identified in the host webs was also skewed (χ^2 Test, $P < 0.05$). In *Architis* sp. webs, most of the *P. republicana* (40 of 63 total) were located in the barrier area (Fig. 3). However, in *A. eximius* webs, *P. republicana* were evenly distributed between areas close to the sheet and barrier areas (Fig. 3). Specifically, the *P. republicana* in the social spider webs were most abundant under the sheet and in the high barrier; and they were least abundant just above the sheet and in the low barrier (Fig. 3). The distributions of *P. republicana* webs in the two host species we observed in 1989 were significantly different from one another (χ^2 Test, $P < 0.05$).
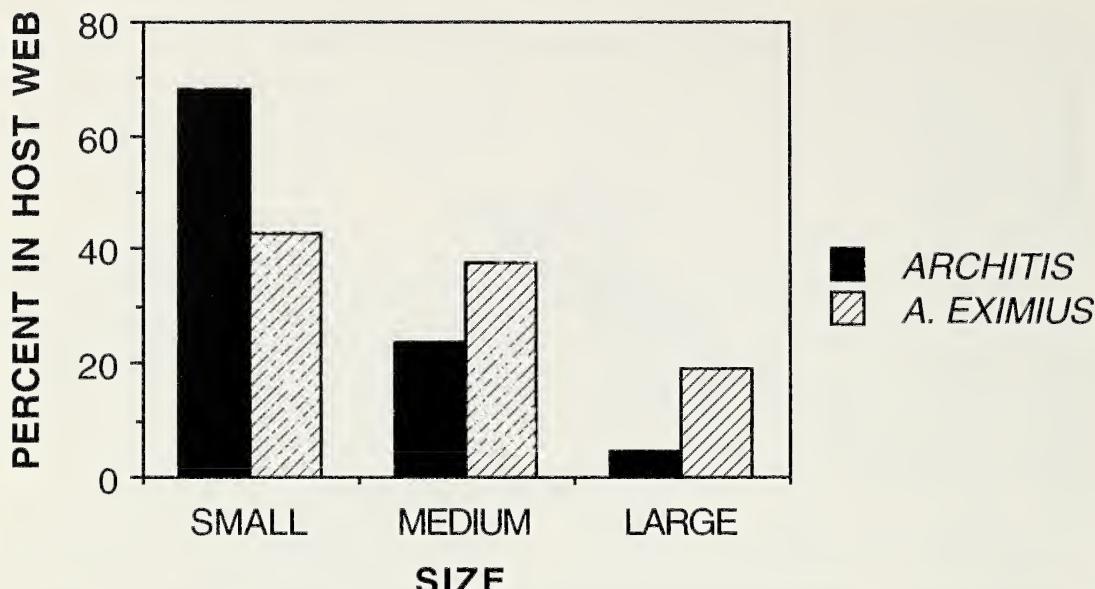
Figure 2.—The size distribution of *Philoponella republicana* individuals in the webs of the two host species, *Architis* sp. and *Anelosimus eximius*. "Small" spiders were all less than 2 mm in length; "Medium" spiders ranged from 2–4 mm in length, and "Large" spiders were between 4–6 mm in length.

We had sufficient data to look specifically at the distribution of the different size classes and their feeding frequencies for *P. republicana* in the social spider webs. Small *P. republicana* were abundant in the high barrier but a very few were located just above the sheet (Fig. 4). Only 15 of the 172 small spiders we censused captured any prey item and fed during our observations, and the distribution of those individuals was not significantly different from the distribution of all small spiders within the host webs (χ^2 Test, $P >$ 0.3) (Fig. 4). Medium-sized *P. republicana* were evenly distributed across the positions within the social spider webs (χ^2 Test, $P > 0.3$); however, those located close to the sheet were more likely to be observed feeding than those in the barrier areas (25 of the 30 spiders that captured prey) (Fig. 4). Forty-seven of the 77 large spiders we observed were located under the sheet of the host web so the distribution of individuals in this size class was not even across the positions (χ^2 Test, $P < 0.05$) (Fig. 4). Twenty-four of the 77 large spiders we censused fed during our observations and 80% of those were located under the sheet (χ^2 Test, $P < 0.05$) (Fig. 4).

Our sample size of *P. republicana* in *Architis* sp. webs was not large enough to make the comparisons of position, size and feeding that we were able to make in the social spider host. Only

5 of the 63 spiders censused in *Architis* sp. webs captured prey, and all of those were spiders in the large size category located in the barrier webbing.

The prey captured by *P. republicana* in these host webs was 2.1 ± 1.2 mm in length which is much smaller than the mean prey size captured by *A. eximius* (5.9 ± 2.1 mm) (Mann-Whitney *U*-Test, $P < 0.05$) (Rypstra 1990). In our prey introduction trials with *Architis* sp., spiders reacted to only 17 of the 112 insects in this size class that we introduced into 10 different webs and the fruit flies were captured on only six occasions. In most of the introductions, the *Architis* web resident did not move at all when the prey were introduced but then would respond to the larger prey item at the end of the trial.

The cribellar silk of the *P. republicana* was able to detain *A. eximius* quite effectively if they happened into one of the webs. On three occasions, a *P. republicana* individual, located in the barrier, successfully captured and killed a penultimate or adult *A. eximius* female. In no case did we observe *A. eximius* capture a *P. republicana*. At dusk, *A. eximius* has a period of web cleaning and maintenance; and, at that time, they would cut out and remove many of the webs of *P. republicana* that were located above the sheet and in the barrier webbing. When they did this, the
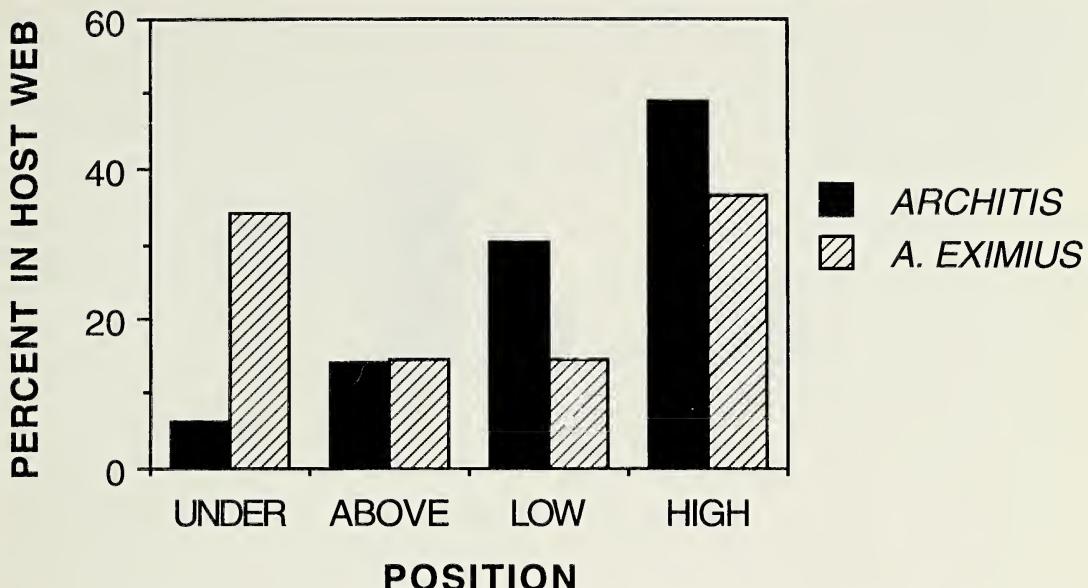
Figure 3.—The distribution of *Philoponella republicana* in the various positions in the host webs. The identified positions were "Under" the sheet, just "Above" the sheet (within 2 cm), in the "Low" barrier webbing (between 2–20 cm above the sheet) and in the "High" barrier (greater than 20 cm above the sheet).

P. republicana would evacuate their web and hang motionless near the location. In only one instance did we observe *A. eximius* destroying a *P. republicana* web located below the sheet during this activity.

DISCUSSION

Our observations suggest that *P. republicana* is a commensal in the webs of *A. eximius* and *Architis* sp. since they capture prey much smaller than those captured by the host species. They appear to use the webs of other species as support, perhaps to enable them to locate their small orb webs in areas otherwise unavailable to them. It is also possible that the webs of the host species enlarge the effective size of their own web allowing them to detect insects sooner and at a greater distance. Perhaps there is some ricochet effect as small insects are deflected and detained by strands of the large host web which could increase the rate of capture by the commensal spider (Uetz 1989). Bradoo (1986) observed *U. ferokus* moving out of their orbs to capture prey on the surface of the host web but we never observed this sort of behavior by *P. republicana*. Bradoo's (1986) descriptions suggest that the relationship between that commensal and its social spider host is much more interdependent than that which

we observed between *P. republicana* and *A. eximius*.

There are more commensals located in the social spider webs than in the solitary spider's web. Likewise, as the social spider web becomes larger more potential web sites are formed and more *P. republicana* colonize them resulting in a correlation between their number and web size. However, even though more web sites would presumably be available as the *Architis* webs increased in size as well, no additional commensal spiders colonized them. We suspect that the increased activity in the social webs deflects more prey into the commensal's webs, which would make those sites preferable. Unfortunately, prey capture by *P. republicana* in *Architis* sp. webs was sufficiently uncommon in our observations that we cannot verify that difference statistically. The fact that there were more large individuals in the social spider webs suggests that they feed more successfully there. In addition, the fact that they are occasional predators on the host in the social spider's web indicates that more potential food is available there.

On the other hand, the density of commensals in the webs of the social spider may not be related to prey capture at all. At some point in the evolution of sociality, spiders must become more tolerant of other spiders (Kullmann 1972; Wil-
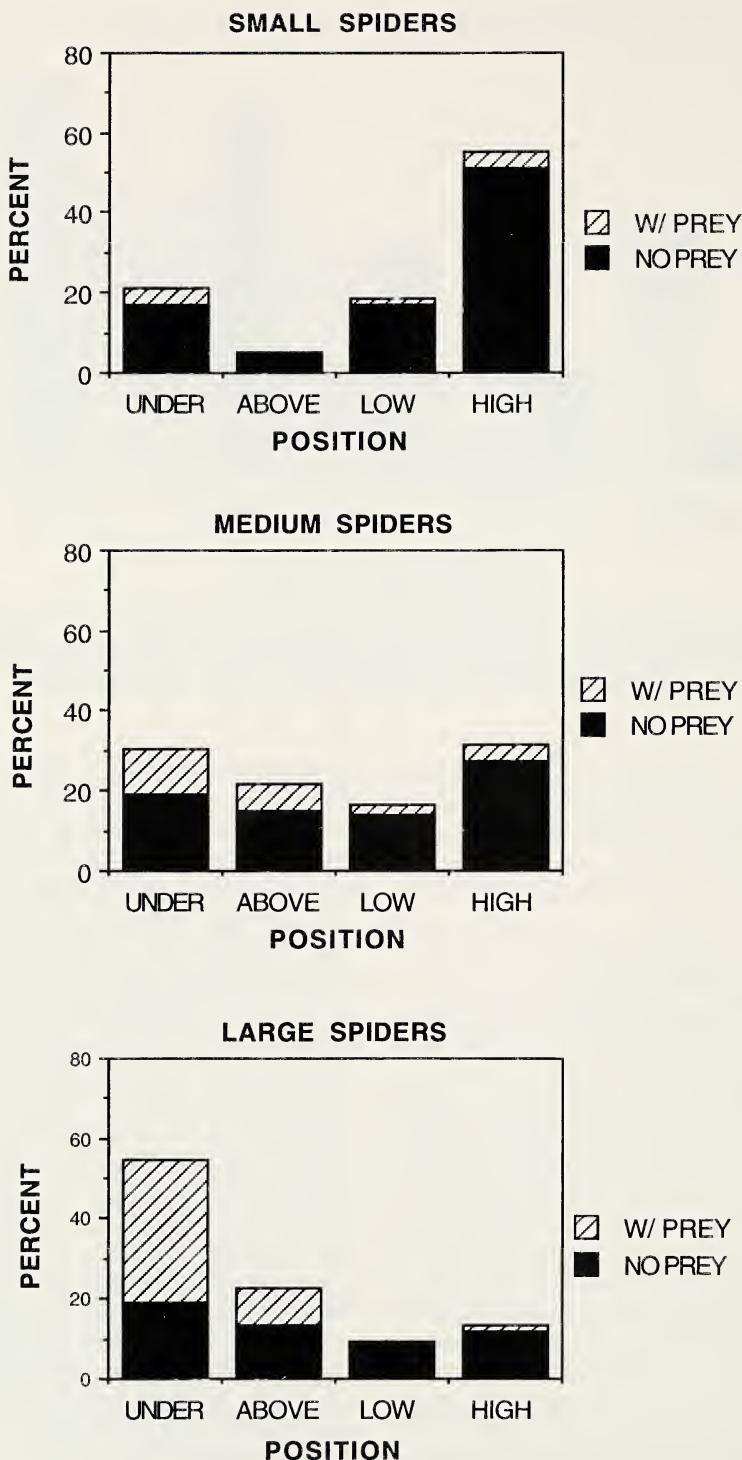
Figure 4.—The distribution of various size classes in the various positions in the social spider webs and the proportion of individuals which were observed to capture prey within a three-hour time period.

son 1975). It may be that *A. eximius* webs are easier to colonize because of this factor. The social spider regularly associates with lots of other spiders and therefore must have relaxed its aggressive tendencies toward them, whereas the solitary species can afford to rid aggressively its web of all other spiders indiscriminately except during the restricted circumstances when it is being courted by a male. The fact that the social species is predisposed to tolerate other spiders may mean that it is easier for heterospecific relationships to perpetuate in their company.

Locations under the sheet in the social spider's webs seem to attract the largest *P. republicana*, and those locations also seem to be the areas of highest prey capture (Fig. 4). It could be that juveniles that happen to select web sites in that location capture more prey and thereby grow large more quickly and/or remain longer in the host web that those in other areas. It is also possible that, as the spiders grow, they are more able to compete for these high quality sites. Our data suggest that sites under the sheet afforded both higher prey capture rates and more protection from disturbance in the host webs of the social spider. One disadvantage to these sites may be that *P. republicana* that located there would encounter fewer of the social spider individuals and therefore be less successful as a predator.

It is curious to note that we never found an adult in the interstices of these complex host webs, even though adults were present in at the study site at the time these data were collected. Interestingly, in our study area we found adults only in aggregations composed exclusively of *P. republicana* individuals. Lubin (1980) suggested that the single species aggregations of *P. republicana* were sibling groups arising from a single egg case, and our surveys of *P. republicana* colonies over the years support that idea (unpub. data). However, we have also observed that a large number of juveniles are commensals for some portion of their life. If this commensal state is a phase that many juveniles pass through, then it would be interesting to discover what cues they use to reaggregate with conspecifics in this complicated habitat. Nyffleler & Benz (1980) report that juvenile stages of several other species of orb weavers act as kleptoparasites and commensals in the webs of other spiders. They consider the commensal relationship as a transition to a more invasive kleptoparasitism. We have already mentioned the more active prey capture out of the host web that Bradoo (1986) reports

for *U. ferokus* which suggests that there is a continuum of dependence on other spider species within the family Uloboridae. It is important to conduct more detailed studies of these relationships in order to understand more fully the evolution of these various behavior patterns.

ACKNOWLEDGMENTS

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NEW SPECIES AND RECORDS OF THE
GROUND SPIDER FAMILY GALLIENIELLIDAE
(ARANEAE, GNAPHOSOIDEA) FROM MADAGASCAR

Norman I. Platnick: Department of Entomology, American Museum of Natural History; New York, New York 10024 USA

ABSTRACT. The females of *Gallieniella blanci* Platnick and *Legendrena perinet* Platnick are described for the first time, as are two new species: *Legendrena rothi* and *Legendrena spiralis*.

Recent fieldwork in Madagascar by several colleagues has resulted in much new information on the unusual ground spiders of the family Gallieniellidae, once thought to be endemic to that island but now known also from the Comoro Islands, Africa, and Australia (Platnick 1990a). As the Malagasy members of the family have been treated by Platnick (1984, 1990b, 1993), it seemed best to update that coverage by supplying new records and describing newly discovered taxa. Material was kindly made available from the collections of the California Academy of Sciences, San Francisco (CAS), by Charles Griswold and Darrell Ubick, the Museum of Comparative Zoology, Harvard University (MCZ), by Herbert Levi and Laura Leibensperger, and the National Museum of Natural History, Smithsonian Institution (USNM) by Jonathan Coddington and Scott Larcher. The illustrations are by Mohammad Shadab of the American Museum of Natural History. The format of the descriptions follows that of the original revision (Platnick 1984); all measurements are in mm.

Gallieniella mygaloides Millot

New records. — MADAGASCAR. *Fianarantsoa:* Maharira summit, Ranomafana National Park, Apr. 9, 1992 (Albert, MCZ), 1♀; Ranomafana National Park, Apr. 1992, pitfall trap (V., B. Roth, CAS), 1♂1♀.

Gallieniella blanci Platnick
(Figs. 1, 2)

Note. —-The female here assigned to this species was not taken with a male, but is paired on the basis of genitalic similarities of both males and females to those of *G. mygaloides* (Figs. 1, 2).

Diagnosis. —The newly described female can easily be separated from those of the other known species by the relatively large spermathecae, which approach the coiled anterior ducts in size.

Female. —Total length, not including chelicerae, 4.57. Carapace 2.00 long, 1.92 wide, dark chestnut brown; pars thoracica with recumbent white scales. From above, anterior eye row recurved, posterior row slightly recurved; from front, both rows very slightly procurved; eye sizes and interdistances: AME 0.06, ALE 0.08, PME 0.06, PLE 0.05; AME-AME 0.13, AME-ALE 0.03, PME-PME 0.15, PME-PLE 0.06, ALE-PLE 0.07; MOQ length 0.20, front width 0.25, back width 0.27. Clypeal height at AME about 1.6 times their diameter. Chelicerae extending forward distance about one-third of carapace length, bearing long fang without distinct ventral tubercle but abruptly narrowed at about one-third its length, narrow portion much paler than thicker portion; most distal promarginal tooth widely separated from other two subequal teeth, all promarginal teeth larger than two widely separated retromarginal teeth. Leg spination: femora II–IV d1-0-0; tibiae: III p0-1-0, v2-2-0, r0-1-0; IV p0-0-1, v4-2-2, r0-0-1; metatarsus IV v1p-0-0. Legs light brown except sides of femora I, II, IV light yellow. Abdomen dark gray, dorsum with two longitudinal white stripes at sides, stripes connected posteriorly by seven chevrons; venter paler than sides. Palpal femur and more distal segments with dorsal spines grading into bristles, tibia and tarsus each with proximal prolateral spine as well. Spermathecae almost as large as anterior, coiled epigynal ducts (Figs. 1, 2).

New record. —MADAGASCAR. *Toliara:* Mahafaly, nr. Eleotse, by Lac Tsimanampetsoa, 24°10′S, 43°45′E, Sept. 15–16, 1992 (V., B. Roth, CAS), 1♀.
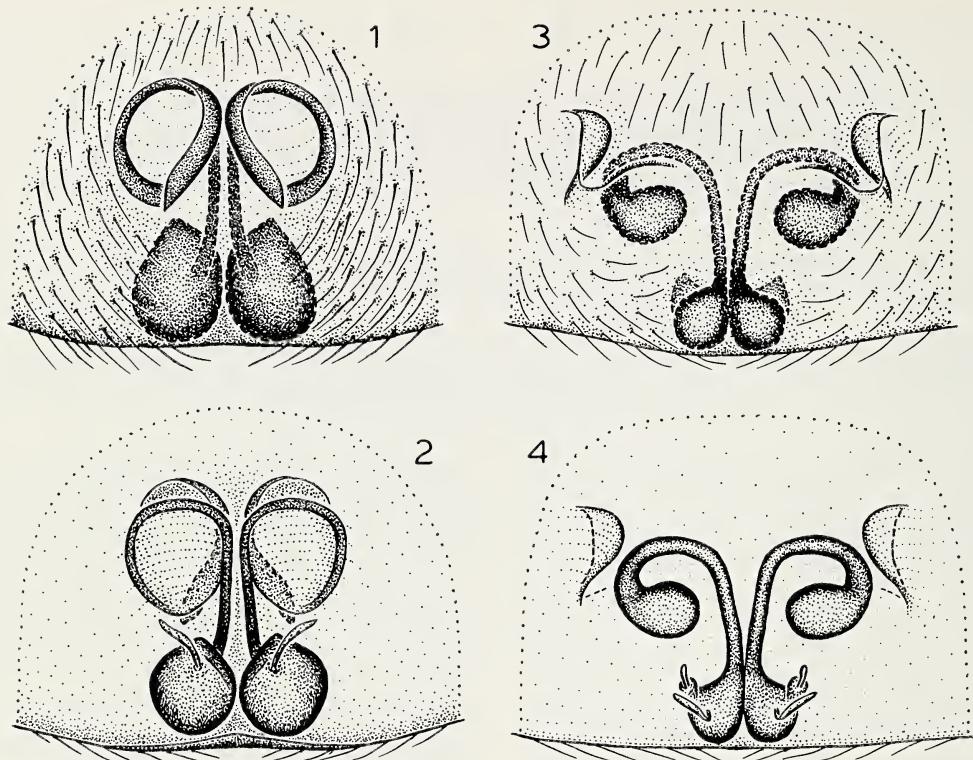
Figures 1–4.—1, 2. *Gallieniella blanci* Platnick, epigynum: 1, ventral view; 2, dorsal view. 3, 4. *Legendrena perinet* Platnick, epigynum: 3, ventral view; 4, dorsal view.

Legendrena perinet Platnick
(Figs. 3, 4)

Diagnosis.—Females can be recognized easily by the anteriorly curled epigynal ducts (Figs. 3, 4).

Female.—Total length, not including chelicerae, 3.50. Carapace 1.84 long, 1.52 wide, light brown, without scales. From above, anterior eye row recurved, posterior row slightly recurved; from front, anterior row very slightly recurved, posterior row slightly procurved; eye sizes and interdistances: AME 0.06, ALE 0.09, PME 0.08, PLE 0.09; AME-AME 0.06, AME-ALE 0.01, PME-PME 0.11, PME-PLE 0.04, ALE-PLE 0.03; MOQ length 0.19, front width 0.18, back width 0.27. Clypeal height at AME only slightly greater than their diameter. Chelicerae extending forward distance greater than one-third of carapace length, bearing relatively short fang without ventral tubercle but slightly narrowed, lightened at about one-third its length; three promarginal teeth closely spaced, middle one largest; two retromarginal teeth enlarged, widely separated. Leg spination: femora I–IV d1-0-0. Femora, patellae,

and tibiae light brown except distal half of tibia I and distal tip of tibiae III, IV lightened; metatarsi and tarsi light orange. Abdomen dark gray, dorsum unmarked, venter with two pale longitudinal stripes near sides. Palpal femur and more distal segments with dorsal spines grading into bristles, tibia and tarsus each with proximal prolateral spine as well. Epigynum with pair of anterolateral pockets (Fig. 3), ducts curling anteriorly (Fig. 4).

New records.—MADAGASCAR. *Fianarantsoa*: Ranomafana National Park, Apr. 1992, pitfall trap (V., B. Roth, CAS), 3♂3♀; 200 m N research cabin, Ranomafana National Park, Mar. 25, 1992, in leaf litter (S. Kariko, V. Roth, MCZ), 1♂1♀.

Legendrena steineri Platnick

New records.—MADAGASCAR. *Fianarantsoa*: 7 km W Ranomafana, Feb. 23–28, 1990, elev. 900 m, flight intercept-yellow pan trap in malaise trap in small clearing, montane rain forest (W. E. Steiner, USNM), 1♂; Ranomafana National Park, Apr. 1992, pitfall trap (V., B. Roth,
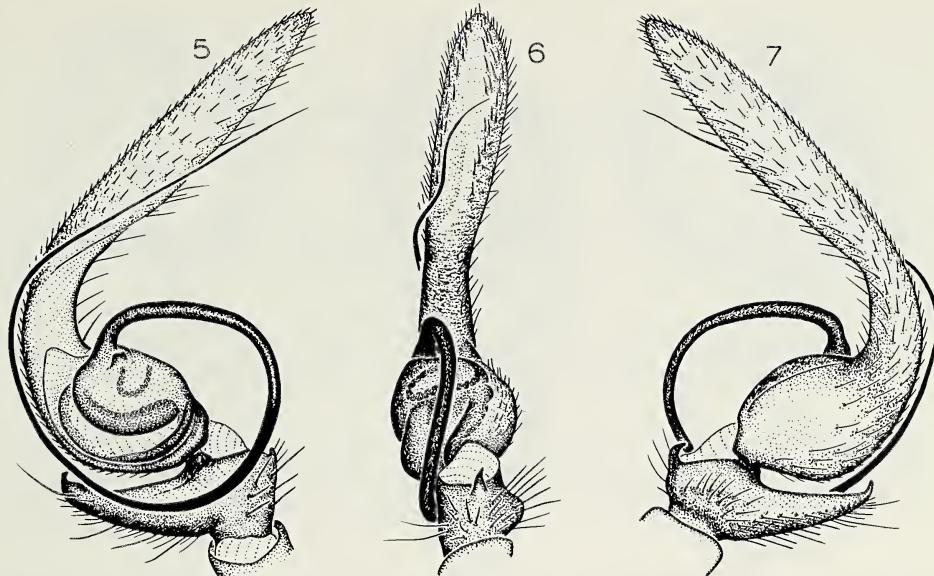
Figures 5–7.—*Legendrena rothi* new species, left male palp: 5, prolateral view; 6, ventral view; 7, retrolateral view.

CAS), 1♂1♀, May 1992 (S. Kariko; V., B. Roth, CAS), 1♀; Ranomafana National Park, ca. 21°12'S, 47°27'E, Mar.–Apr. 1992, forest foliage (V., B. Roth, MCZ), 1♀, Apr. 1992, forest (V., B. Roth; S. Kariko, CAS), 1♀.

Legendrena rothi new species
(Figs. 5–7)

Type.—Male holotype from Claire's camp, Vatoaranana, Ranomafana National Park, Fianarantsoa, Madagascar (May 9, 1992; V. Roth), deposited in CAS.

Etymology.—The specific name is a patronym in honor of the collector.

Diagnosis.—The basally incrassate tibia I, palpal tibial apophysis bearing cusps, and elongate embolus indicate that this is the sister species of *L. steineri*, from which it differs in having the embolus originating distally, rather than proximally, on the palpal bulb (Figs. 5–7).

Male.—Total length, not including chelicerae, 5.19. Carapace 2.14 long, 1.62 wide, dark chestnut brown, without scales. From above, anterior eye row recurved, posterior row slightly recurved; from front, both rows very slightly procurved; eye sizes and interdistances: AME 0.07, ALE 0.09, PME 0.08, PLE 0.07; AME-AME 0.08, AME-ALE 0.03, PME-PME 0.14, PME-PLE 0.04, ALE-PLE 0.04; MOQ length 0.18, front width 0.22, back width 0.30. Clypeal height at

AME only slightly greater than their diameter. Chelicerae extending forward distance less than one-third of carapace length, bearing relatively short fang without ventral tubercle but slightly narrowed, lightened at about half its length; three promarginal teeth closely spaced, middle one largest; two retromarginal teeth enlarged, widely separated. Leg spination: femora III, IV d1-0-0. Coxae and trochanters yellow; femora dark gray, I–III with dorsal yellow longitudinal stripe; patella I dark gray, II, III yellow with lateral dark stripes; IV yellow; tibia I incrassate, dark gray, with ventral fringe of long setae proximally, yellow distally, other tibiae yellow with dark lateral longitudinal stripes; anterior metatarsi and tarsi light orange, posteriors yellow. Abdomen dark gray, dorsum without distinct scutum, with vaguely indicated transverse white stripe at about one-third its length. Palpal tibia with elongate dorsal apophysis bearing retrolateral row of cusps; embolus originating distally, extending almost to tip of elongated cymbium (Figs. 5–7).

Female.—Unknown.

Distribution.—Known only from southeastern Madagascar.

Legendrena spiralis new species
(Figs. 8–10)

Type.—Male holotype taken on foliage along Namorona River, Ranomafana National Park,
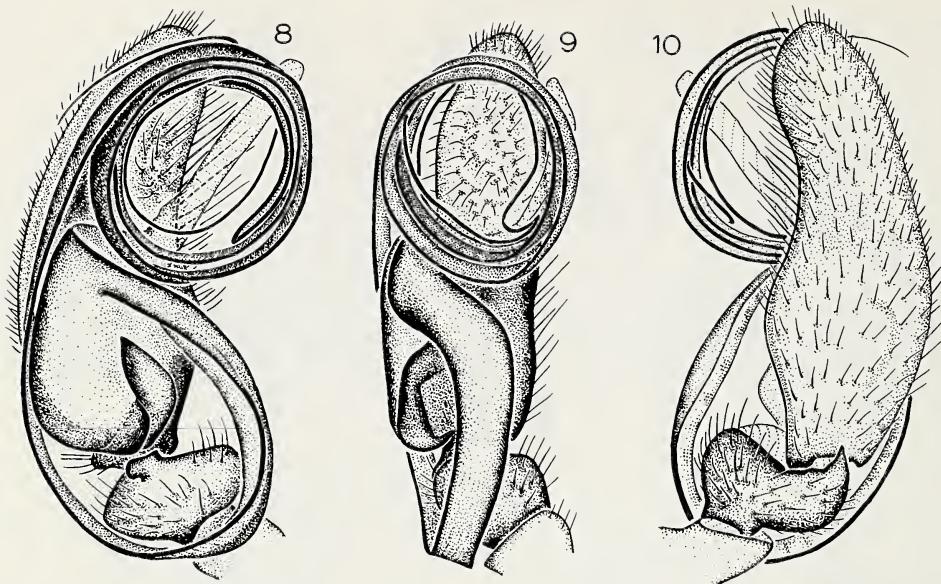
Figures 8–10.—*Legendrena spiralis* new species, left male palp: 8, prolateral view; 9, ventral view; 10, retrolateral view.

Fianarantsoa, Madagascar (May 18, 1992; B. Roth), deposited in CAS.

Etymology.—The specific name refers to the coiled embolus.

Diagnosis.—Males can easily be separated from those of the other known species by the distally coiled embolus (Figs. 8–10).

Male.—Total length, not including chelicerae, 3.89. Carapace 1.73 long, 1.46 wide, dark chestnut brown, without scales. From above, anterior eye row recurved, posterior row slightly recurved; from front, anterior row slightly recurved, posterior row almost straight; eye sizes and interdistances: AME 0.06, ALE 0.06, PME 0.08, PLE 0.07; AME-AME 0.05, AME-ALE 0.02, PME-PME 0.15, PME-PLE 0.06, ALE-PLE 0.07; MOQ length 0.19, front width 0.23, back width 0.25. Clypeal height at AME only slightly greater than their diameter. Chelicerae extending forward distance less than one-third of carapace length, bearing relatively short fang without ventral tubercle but slightly narrowed, lightened at about half its length; three promarginal teeth closely spaced, middle one largest; two retromarginal teeth widely separated but not enlarged. Leg spination: femora I–IV d1-0-0. Coxae and trochanters yellow, I–III with dark lateral stripes; femora dark gray, I with lateral light stripes along ventral half of sides, II, III with dorsal yellow longitudinal stripe; patella I dark gray, II, III

yellow with lateral dark stripes, IV yellow proximally, dark gray distally; tibia I not incrassate or fringed, dark gray proximally, yellow distally, other tibiae dark orange with dark lateral longitudinal stripes; anterior metatarsi and tarsi light orange, posteriors yellow. Abdomen dark gray, dorsum without distinct scutum, with vaguely indicated transverse white stripe at about one-third its length. Palpal tibia with short, hook-shaped retrolateral tibial apophysis; embolus originating distally, broadened proximally, coiling at tip of cymbium (Figs. 8–10).

Female.—Unknown.

Distribution.—Known only from southeastern Madagascar.

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ON THE SPIDER GENUS *HEBRITHELE*
(ARANEAE, MITURGIDAE)

Norman I. Platnick: Department of Entomology, American Museum of Natural History; New York, New York 10024 USA

Alexandre B. Bonaldo: Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, C. Postal 1188, CEP 90001–970, Porto Alegre RS, Brazil

ABSTRACT. The genus *Hebrithele* has been known only from the female holotype of its type species, *Hebrithele longicauda* Berland. The male of the species was apparently described earlier but was misplaced in the family Gnaphosidae. *Hypodrassodes insulanus* (Rainbow) is transferred to the Miturgidae and considered a senior synonym of *Hebrithele longicauda*.

The spider genus *Hebrithele* was established by Berland (1938) on the basis of a single female from the New Hebrides. Berland considered the spider of ambiguous relationship, noting that the widely separated anterior lateral spinnerets suggested a placement in the Gnaphosidae, where the enlarged anterior median eyes suggested possible relationships to such genera as *Leptodrassus* Simon or *Anzacia* Dalmas. However, the presence of a long distal segment on the posterior lateral spinnerets made Berland hesitant to assign the genus to the Gnaphosidae, as gnaphosids do not share that feature. He therefore assigned the genus to the Clubionidae, suggesting a close relationship to such New World genera as *Eutichurus* Simon and *Strotarchus* Simon, both of which are currently assigned to the Miturgidae. *Hebrithele* was itself transferred to the Miturgidae by Lehtinen (1967), who did not assign the genus to any of the six miturgid subfamilies that he recognized (although he suggested a possible placement in the otherwise New World Eutichurinae).

During a recent visit to the B. P. Bishop Museum in Honolulu, the first author encountered, among Pacific spiders identified as gnaphosids, a male from the New Hebrides that seemed to belong to *Hebrithele*. A subsequent literature search indicated that this male was probably first described by Rainbow (1901) as the gnaphosid *Leptodrassus insulanus*. The holotype of that species, unfortunately, appears to be lost; it is not in the collection of the Australian Museum, Sydney, even though the remaining types from that paper are housed there (Dr. M. R. Gray, *in litt.*). Nevertheless, Rainbow's figure of the male palp is detailed enough to leave few doubts about its identity with the Bishop Museum specimen.

Rainbow's species was later transferred to the gnaphosid genus *Anzacia* Dalmas by Dalmas (1919). For unknown reasons, the species was transferred by Roewer (1955) to the gnaphosid genus *Hypodrassodes* Dalmas.

Examination of both sexes leads us to concur with Lehtinen on the placement of *Hebrithele* within the Miturgidae. We do not concur with his tentative placement of the genus in the subfamily Eutichurinae, however, as the thoracic groove is well demarcated (rather than reduced or absent) and the retrolateral margin of the cymbium has an incision, rather than the projection typical of eutichurines (see Bonaldo 1994). Both the incised cymbium and the widely separated anterior lateral spinnerets suggest a placement in the Miturginae, closer to the American genera *Teminius* Keyserling (see Platnick & Shadab 1989) and *Strotarchus* Simon (transferred from the Eutichurinae to the Miturginae by Bonaldo 1994), and the Australasian genus *Miturga* Thorell, rather than in the Eutichurinae.

All measurements are in millimeters.

Hebrithele Berland

Hebrithele Berland 1938: 137 (type species by original designation *Hebrithele longicauda* Berland).

Diagnosis.—The combined presence of an elongated distal segment on the posterior lateral spinnerets, widely separated anterior lateral spinnerets, a well-marked thoracic groove (Figs.
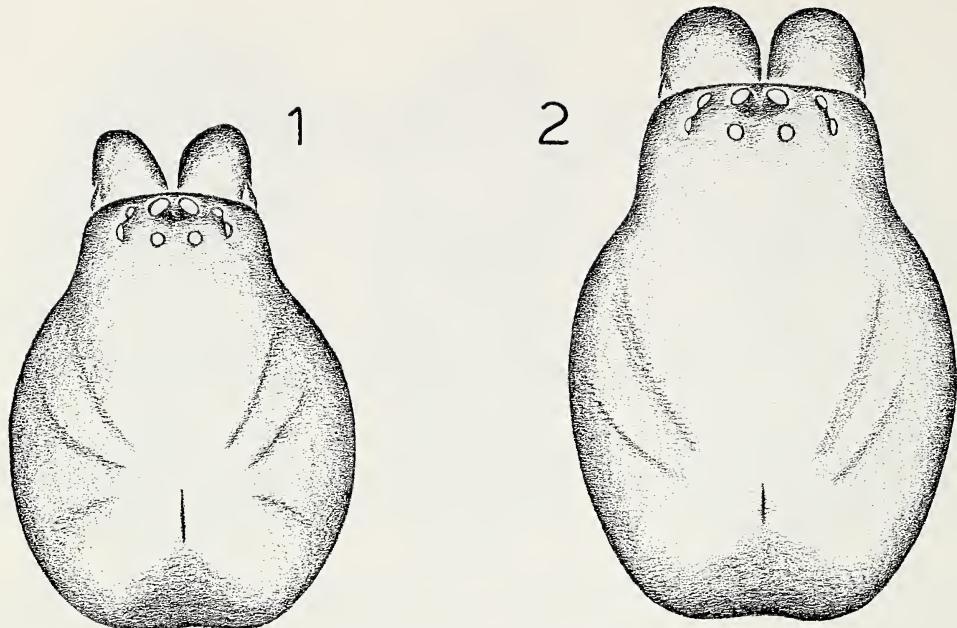
Figures 1, 2.—*Hebrithele insulana* (Rainbow), carapace, dorsal view. 1, male; 2, female.

1, 2), an incised cymbial margin (Fig. 4), a palpal bulb lacking a median apophysis, and large, ovoid spermathecae (Fig. 6) is diagnostic of the genus.

Description.—Araneomorph, ecribellate, entelegyne spiders. Carapace widest between coxae II and III, narrowed opposite palpal insertion, light brownish orange; cephalic area flattened, thoracic groove longitudinal, long, occupying over one-sixth of carapace length; ocular area and clypeus with numerous weak, white setae and several strong bristles. From above, anterior eye row recurved, posterior row procurved; from front, both rows procurved; all eyes circular, AME much larger than others; PME and PLE subequal, smaller than ALE; AME separated by less than their radius, by less than their radius from ALE; PME separated by about twice their diameter, by more than their diameter from PLE; ALE and PLE almost contiguous; MOQ about as wide in front as in back, wider than long; clypeal height slightly greater than AME diameter; chilum present as distinct triangular sclerite. Chelicerae usually with three promarginal teeth, median one largest, situated near tip of fang furrow; three smaller retromarginal teeth situated closer to base of fang, with tooth closest to fang smaller than others (or missing). Mouthparts and sternum light brown, darkest at base of labium and endites; endites distally squared in males (distal margin of female endites more rounded),

without oblique depressions, with strong serrula, extending far beyond labium; labium only slightly longer than wide, invaginated at posterolateral corners; sternum shield-shaped, not rebordered, with sclerotized extensions to each coxa and between coxae I and II. Leg formula 4123; legs light brownish orange; tarsi with two dentate claws and conspicuous claw tufts; trochanters deeply notched; trichobothria present on tibiae, metatarsi, and tarsi. Abdomen brownish gray, coated with strong, dark setae; males without dorsal scutum; anterior lateral spinnerets elongated, separated at base by almost their diameter, with distinct distal segment bearing one major ampullate gland spigot and several piriform gland spigots not enlarged in either sex; posterior median spinnerets short, tubular in both sexes; posterior lateral spinnerets with two long segments; colulus represented by wide setose area of cuticle. Male palp with femur and patella unmodified; tibia with retrolaterally directed retrolateral apophysis; bulb with strong embolus and membranous conductor, without median apophysis. Epigynum wide, heavily sclerotized posteriorly.

Hebrithele insulana (Rainbow) new combination
(Figs. 1–6)

Leptodrassus insulanus Rainbow 1901: 523, pl. XXVIII, figs. 1, 1a (male holotype from Malekula Is., New
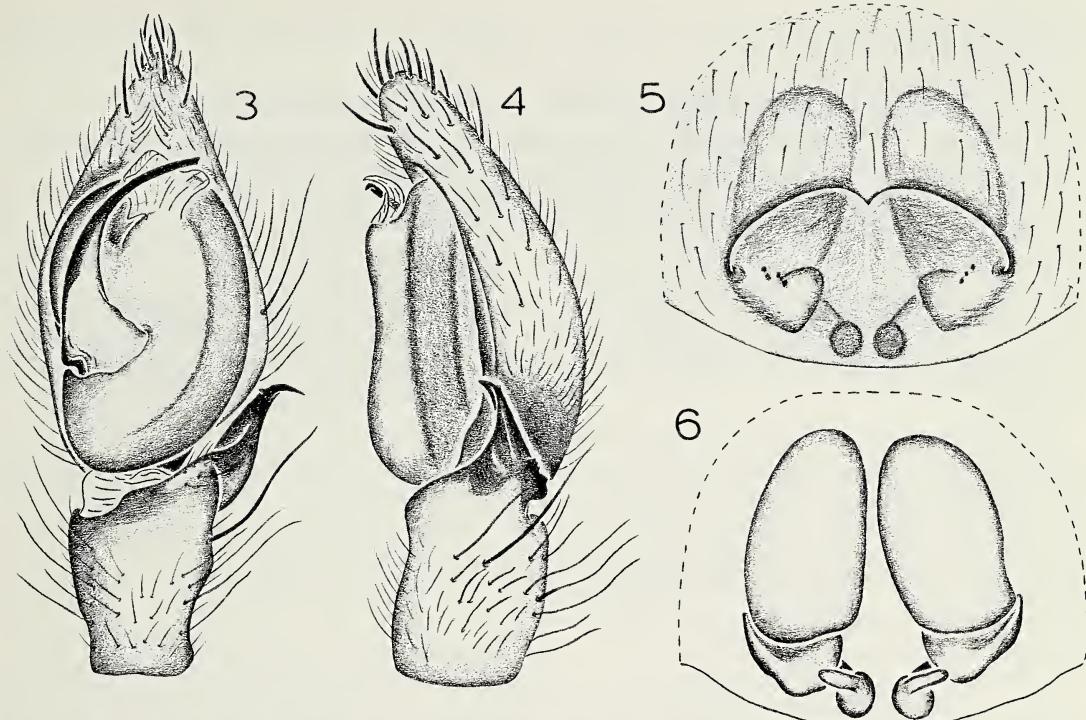
Figures 3–6.—*Hebrithele insulana* (Rainbow). 3, left male palp, ventral view; 4, same, retrolateral view; 5, epigynum, ventral view; 6, same, dorsal view.

Hebrides, should be in the Australian Museum, Sydney, lost).

Anzacia insulana: Dalmas 1919: 249.

Hebrithele longicauda Berland 1938: 137, figs. 21–25 (female holotype from Malekula Is., New Hebrides, in MNHN, examined). NEW SYNONYMY.

Hypodrassodes insulanus: Roewer 1955: 404.

Diagnosis.—The laterally directed retrolateral tibial apophysis of males (Fig. 3) and the arched anterior epigynal margin situated at only half the length of the spermathecae of females (Fig. 5) are presumably diagnostic.

Male.—Total length 7.60. Carapace 3.55 long, 2.75 wide. Eye diameters and interdistances: AME 0.25, ALE 0.15, PME 0.15, PLE 0.17; AME-AME 0.07, AME-ALE 0.05, PME-PME 0.25, PME-PLE 0.22, ALE-PLE 0.05; MOQ length 0.45, front width 0.55, back width 0.52. Chelicerae with three promarginal and three retromarginal teeth. Abdomen 4.05 long, 2.15 wide; posterior lateral spinneret proximal segment 0.75 long, distal segment 0.52 long. Leg measurements (femur, patella, tibia, metatarsus, tarsus, total): I 3.10, 1.50, 2.65, 2.50, 1.25, 11.00; II 2.80, 1.45, 2.30, 2.30, 1.15, 10.00; III 2.50, 1.25,

1.80, 2.25, 1.05, 8.85; IV 3.30, 1.40, 2.70, 3.20, 1.25, 11.85. Leg spination (only surfaces bearing spines listed): femora: I d1-1-1, p0-0-2, r0-0-1; II d1-1-1, p0-1-2, r1-1-1; III, IV d1-1-1, p1-1-1-1, r1-1-1-1; tibiae: I v2-2-1p; II v2-2-2; III, IV d1r-0-0, p1-1, v2-2-2, r1-1; metatarsi: I v2-1r-1r; II v2-2-0; III, IV p1-2-2, v2-2-2, r1-2-2. Retrolateral tibial apophysis with tiny, triangular cusp on medial margin near tip (Fig. 3); embolus strong, arched, supported by membranous conductor (Fig. 4).

Female.—Total length 7.90. Carapace 4.10 long, 3.05 wide. Eye diameters and interdistances: AME 0.22, ALE 0.20, PME 0.15, PLE 0.20; AME-AME 0.15, AME-ALE 0.07, PME-PME 0.32, PME-PLE 0.30, ALE-PLE 0.05; MOQ length 0.52, front width 0.60, back width 0.57. Chelicerae with two (right) or three (left) promarginal and three retromarginal teeth. Abdomen 4.00 long, 2.30 wide; posterior lateral spinneret proximal segment 0.80 long, distal segment 0.60 long. Leg measurements: I 3.20, 1.80, 2.75, metatarsi and tarsi missing; II 3.15, 1.65, 2.40, 2.25, 1.25, 10.70; III 2.80, 1.30, 1.85, 2.25, 0.95, 9.15; IV 3.50, 1.65, 2.85, 3.30, 1.25, 12.55. Leg

spination: femora: I, II d1-1-0; III d1-1-0, p1-1-1, r1-1-1-1; IV d1-1-1, p1-1-1, r1-1-1-1; tibiae: I v2-2-0; II v1p-1p-0; III, IV d1r-0-0, p1-1, v2-2-2, r1-1; metatarsi: I missing; II v2-0-0; III, IV p1-2-2, v2-2-2. r1-2-2. Anterior epigynal margin bipartite, arched (Fig. 5), spermathecae large, oval (Fig. 6).

Material examined.—NEW HEBRIDES. *Epi Island*: Lowekewou, Aug. 31, 1979, elev. 0–100 m (Barnes, Nishida, Gagné, Samuelson, BPBM), 1♂. *Malekula Island*: no specific locality, May 1934 (A. de la Ruë, MNHN), 1♀ (holotype).

Distribution.—Known only from the New Hebrides.

Synonymy.—The male and female differ slightly in endite shape, the relative width of the pars cephalica, and coloration; we attribute the first two differences to sexual dimorphism and the latter one to the holotype being a freshly molted specimen. Until additional species of the genus are found, these specimens are most parsimoniously considered conspecific.

ACKNOWLEDGMENTS

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DISCRIMINACION POR *METEPEIRA SEDITIOSA* (KEYSERLING) (ARANEAE, ARANEIDAE) EN CONDICIONES EXPERIMENTALES SOBRE DOS PRESAS FRECUENTES EN EL MEDIO

Carmen Viera: División Zoología Experimental, Instituto de Investigaciones Biológicas Clemente Estable, Av. Italia 3318, Montevideo, Uruguay; Sección Entomología, Departamento de Biología Animal, Facultad de Ciencias, Tristán Narvaja 1674, Montevideo, Uruguay

ABSTRACT. The predatory behavior of *Metepeira seditiosa* on two prey organisms, *Musca* sp. and *Acromyrmex* sp., was compared under experimental conditions. Frequency diagrams for various behaviors were constructed, and the stereotypy and relationship among the units in the sucession were established. Discrimination between the prey organisms occurred in the detection and immobilization phases. *Metepeira seditiosa* has a vast repertory of behavior. The tactics used for capturing *Musca* sp. and *Acromyrmex* sp. were 100% successful.

RESUMEN. Se describieron y analizaron las secuencias de unidades de comportamiento de captura de *Metepeira seditiosa* frente a dos presas (*Musca* sp. y *Acromyrmex* sp.) en condiciones experimentales. Se realizaron diagramas de frecuencias, estableciéndose las relaciones entre unidades y la presencia de estereotipia en las sucesiones. Se comprobó la discriminación entre las presas mediante la comparación de las Fases de Detección e Inmovilización. *Metepeira seditiosa* posee una amplia gama de unidades de comportamiento con las cuales selecciona la táctica depredadora adecuada ante *Musca* sp. y *Acromyrmex* sp., obteniendo un 100% de éxito en las capturas.

Estudios realizados por Riechert y Luczak (1982), Stowe (1986) y Nentwig (1987), entre otros, han demostrado que las arañas orbitelares exhiben una especialización considerable en la dieta. Peters (1931, 1933) realizó estudios sobre la capacidad que poseen las arañas de distinguir entre diferentes categorías de insectos: Observó que *Araneus diadematus* Clerck atacaba con diferente táctica a moscas vibrantes y moscas inmóviles. Robinson y Robinson (1976) observaron, en por lo menos doce especies de araneidos, discriminación entre lepidópteros y otros insectos; Viera (1981) observó en tres especies diferentes de insectos discriminación en la táctica de ataque y en la eficiencia en la captura de *Alpaida alticeps* (Araneidae).

En cuanto a lo que se sabe sobre *Metepeira* Burgess y Witt (1976) analizaron el diseño de las redes de *Metepeira spinipes* F. Cambridge y *Metepeira labyrinthea* (Hentz) que son similares a las telas de *M. seditiosa*. Viera (1986, 1989) describió cualitativamente y cuantitativamente la red de *M. seditiosa*. Viera y Costa (1985) y Viera (1986, 1994) hicieron aportes sobre el comportamiento de captura. Aún no se han realizado estudios sobre el comportamiento discriminatorio de presas.

Acorde con observaciones realizadas en el campo, por la autora, fueron seleccionados dos representantes de los órdenes Diptera e Hymenoptera como las presas más frecuentes observadas en las redes y capturadas por *M. seditiosa* para ser entregadas en condiciones experimentales.

METODOS

Para este estudio se recolectaron 53 ejemplares en Punta Espinillo (Montevideo, Uruguay) en abril de 1990. Las arañas fueron criadas en el laboratorio en recipientes individuales de vidrio transparente de 14 cm de altura y 9 cm de diámetro, cubierto con una malla de nailon, con un recipiente con agua y un bastidor de madera para soporte de la tela. En los períodos interexperimentales los ejemplares fueron alimentados con trozos de larvas de *Tenebrio* sp. (Coleoptera). Durante el período de cría y experimentación la temperatura media diaria fue 22.5 ± 2.67 °C

y el fotoperíodo de 12 h luz y 12 h oscuridad. Las presas utilizadas fueron *Musca domestica* (Diptera) y *Acromyrmex* sp. (Hymenoptera). El tamaño de todas las presas fue similar o ligeramente inferior al de la araña.

Para las experiencias se utilizaron sólo individuos juveniles grandes y hembras adultas; los machos adultos se descartaron por su incapacidad para construír telas orbiculares (Viera y Costa 1985). Se formaron dos grupos de 7–8 arañas cada uno, utilizándose una única vez frente a cada presa. Las arañas se trasladaron, cinco días antes de cada experiencia, a recipientes de vidrio transparente de 30 cm de altura, 30 cm de ancho y 10 cm de fondo, con una cara móvil y un bastidor con un soporte central para sostener la tela y un recipiente con agua. Las observaciones se hicieron desde la entrega de la presa hasta la ingestión, abandono de la misma, o inmovilidad total de la araña por más de 30 min. Las presas fueron entregadas siempre en el mismo lugar aproximado de la tela (zona inferior, ligeramente a la derecha), según el siguiente cronograma: En la primera semana de experimentación se le entregó al grupo A la presa *Musca* sp. En la segunda semana se le entregó al grupo B la presa *Acromyrmex* sp. En la tercera semana se le entregó al grupo B la presa *Musca* sp. En la cuarta semana se le entregó al grupo A la presa *Acromyrmex* sp.

En las observaciones, se colocó una cartulina negra detrás del recipiente y se iluminó lateralmente. Las arañas permanecieron dos días después de la observación, en los recipientes de experimentación para controlar la eliminación de restos de presas y/o reparación de la tela. Todas las experiencias fueron relatadas y registradas en un grabador magnetofónico, midiéndose la duración de las unidades de comportamiento. El comportamiento de captura se dividió en 16 unidades de comportamiento agrupadas en tres fases: a) de Detección, b) Inmovilización, y c) Terminal. Se utilizaron las unidades Tensamiento, Envolvimiento, Corte de Hilos, Transporte y Manipulación Preingestiva descriptas por Robinson y Olazarri (1971). Las unidades Desplazamiento I, Desplazamiento II, Quietud, Acicalamiento, Toqueteo, Mordeduras Cortas y Mordedura Prolongada fueron descriptas por Viera (1983, 1986). Las unidades Fijación y Giro, Fijación de Hilos, Otros Desplazamientos y Recuperación de la Presa fueron descriptas por Viera (1994).

En el análisis estadístico se utilizó el test de diferencias de medias (*t* de Student), con restricciones para la varianza (*F* de Snedecor) y el paquete estadístico PRESTA.

Los ejemplares estudiados se depositaron en la colección aracnológica del Departamento de Entomología de la Facultad de Ciencias, Montevideo.

RESULTADOS

En la captura frente a *Acromyrmex* sp. (Fig. 1) la Fase de Detección se inició mayoritariamente con Tensamiento (14 en 15) que realizaron en el refugio y luego en el centro de la tela. La Fase de Inmovilización se inició exclusivamente con la unidad Envolvimiento que fue sucedida frecuentemente por Mordeduras Cortas. Envolvimiento y Mordeduras Cortas se vincularon en menor medida con Mordedura Prolongada. La Fase de Inmovilización se vinculó con la Fase Final por medio de la sucesión Envolvimiento - Corte de Hilos. La unidad Acicalamiento tuvo una frecuencia alta (9 en 15), relaciónándose con las Fases de Inmovilización y Final. La unidad Otros Desplazamientos tuvo también una frecuencia alta (12 en 15). La unidad Quietud fue la más frecuente (27 veces).

En la captura frente a *Musca* sp. (Fig. 2) realizaron Tensamiento en el refugio (13 en 15) como primera unidad de la Fase de Detección y luego en el centro de la tela. Se observó una alteración a esa sucesión en cinco individuos que no realizaron Tensamiento en el centro de la tela y luego de Desplazamiento II, realizaron Toqueteo. El pasaje de la Fase de Detección a la Fase de Inmovilización se realizó desde Toqueteo. La primera unidad de esta Fase fue mayoritariamente Mordeduras Cortas. Se observó una vinculación menor entre la dupla Envolvimiento - Mordeduras Cortas que entre Envolvimiento - Mordedura Prolongada sólo en esa dirección.

Corte de hilos se vinculó principalmente con Envolvimiento. Dentro de la Fase Final se observó una marcada estereotipia en la sucesión de unidades. La unidad Quietud se vinculó principalmente con Envolvimiento. Aunque se observó 23 veces, las sucesiones fueron múltiples, pero con frecuencias menores al 1% del total de las unidades, no apareciendo por ese motivo en el diagrama. La unidad Acicalamiento se observó ocho veces y se vinculó a unidades de la Fase de Inmovilización.

Análisis comparativo del comportamiento de captura: (Figs. 1, 2). Se compararon los comportamientos de captura ante la misma presa
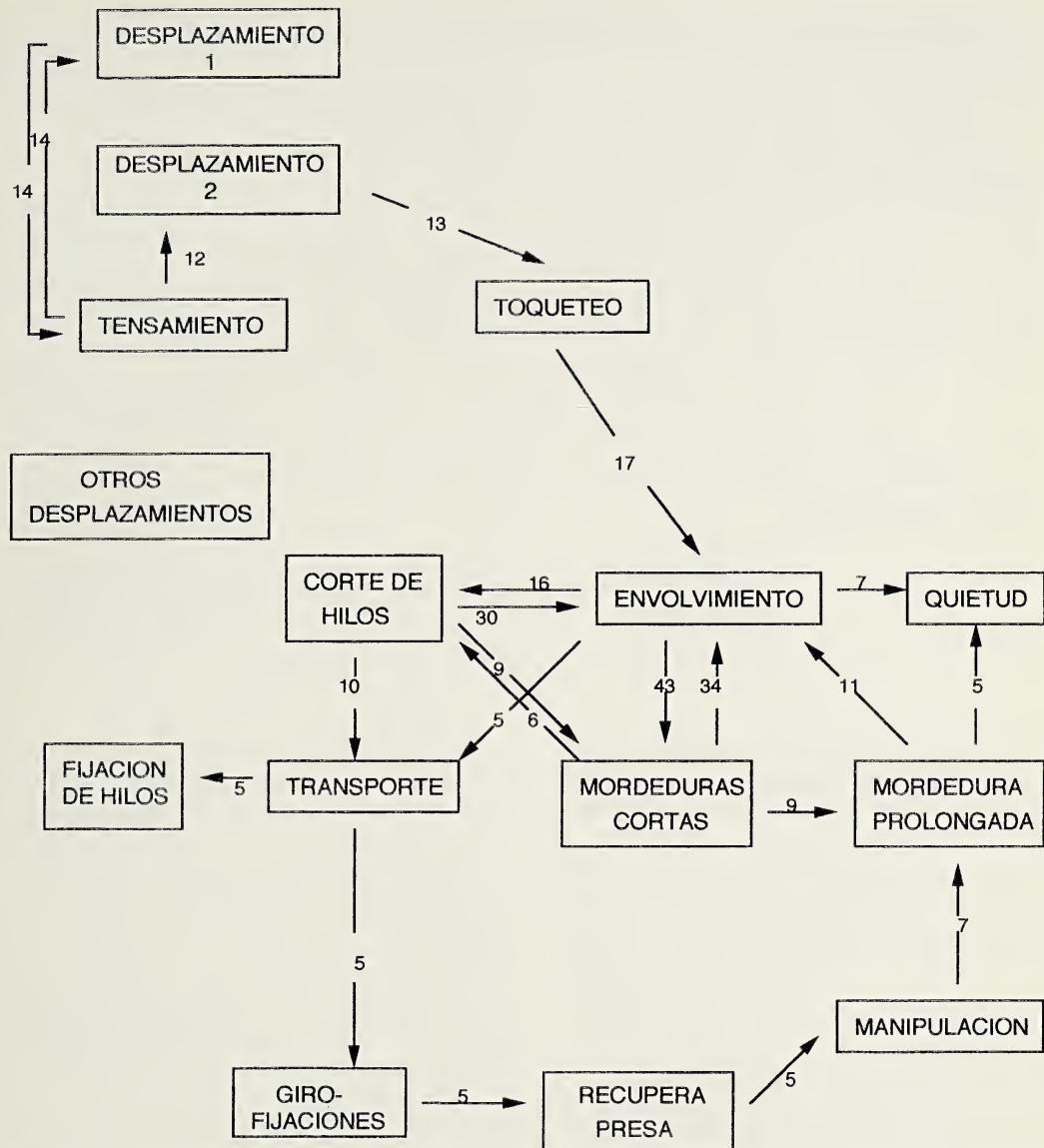
Figura 1.—Diagrama de frecuencias de la captura frente a *Acromyrmex* sp.; *n* = 15, numero total de unidades = 430. Se excluyeron de la figura las frecuencias inferiores o iguales al 1% del total de las unidades.

entre los dos grupos experimentales utilizando las siguientes variables: a) Tiempo de latencia (período que va desde la entrega de la presa hasta la primera respuesta de la araña); b) Duración total del comportamiento de captura; c) Número total de unidades; d) Duración de la Fase de Detección; e) Número de unidades que componen la Fase de Detección; f) Duración de la Fase de Inmovilización; g) Número de unidades que componen la Fase de Inmovilización; h) Duración de las unidades que componen la Fase Final;

i) Número de las unidades que componen la Fase Final.

En las Tabla 1 se pueden observar diferencias estadísticamente significativas entre las duraciones totales de la captura frente a *Musca* sp. y *Acromyrmex* sp.

Asimismo se observaron diferencias estadísticamente significativas en la duración de la Fase de Inmovilización entre las capturas de *Musca* sp. y *Acromyrmex* sp.

Para comprobar que la entrega aleatoria de
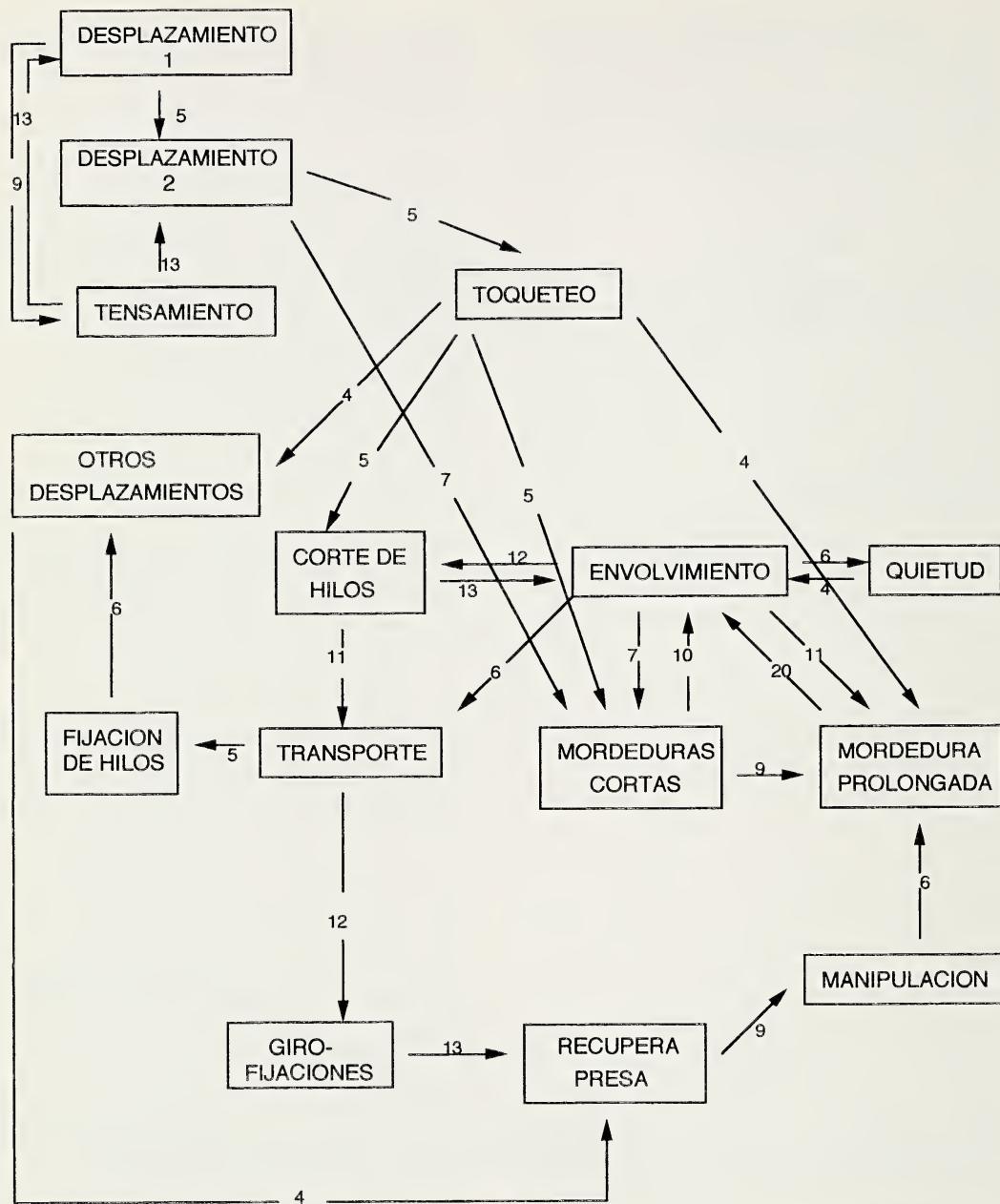
Figura 2.—Diagrama de frecuencias de la captura frente a *Musca* sp.; n = 15, numero total de unidades = 340. Se excluyeron de la figura las frecuencias inferiores o iguales al 1% del total de las unidades.

presas a los grupos de individuos A y B descartarían la posible influencia del aprendizaje en el comportamiento de captura se realizaron test de diferencias de medias con restricciones para la varianza en los dos grupos de experimentación frente a cada tipo de presa. Las variables utilizadas en la comparación fueron: tiempo de latencia, duración total de la captura y número

total de unidades. El test no refleja diferencias estadísticamente significativas (Tabla 2).

Se observó un 100% de éxito en la captura de ambas presas.

DISCUSION

Viera (1983) y Viera y Costa (1985) comprobaron experimentalmente que el comportamien-

Tabla 1.—Valores para nueve variables del comportamiento deltotal de los individuos frente a *Acromyrmex* sp. y *Musca* sp. (*n* = 15). Los tiempos están dados en segundos. Valores de *t* de Student y probabilidades en la comparación.

	Acromyrmex		Musca			
	$\bar{x}$	DT	$\bar{x}$	DT	t	p
1. Tiempo de latencia	98.53	149.41	212.27	325.74	1.187	0.248
2. Duración total de la captura	633.00	421.17	345.00	243.83	2.214	0.035
3. Número total de unidades	28.67	11.88	22.86	9.16	1.446	1.557
4. Duración de detección	33.13	32.47	57.93	99.37	0.888	0.609
5. Número de unidades de detección	3.87	1.63	2.27	1.61	2.614	0.014
6. Duración de inmovilización	436.60	351.20	188.80	118.30	2.502	0.021
7. Número de unidades de inmovilización	13.13	6.60	7.33	6.29	2.816	0.009
8. Duración de fase final	89.53	81.18	102.13	69.23	0.463	0.651
9. Número de unidades de fase final	1.67	1.01	2.13	0.88	1.300	0.202

to de captura en hembras adultas y juveniles de *Metepeira seditiosa* era similar. Esto justificó la utilización de ambos conjuntos como un grupo homogéneo.

Robinson y Robinson (1976) demostraron la influencia del aprendizaje en un segundo encuentro con la misma presa. La ausencia de diferencias estadísticamente significativas en la captura sobre la misma presa en *Metepeira seditiosa* permitió descartar la posibilidad de que, las capturas previas de cada araña, modificaran la siguiente; así como el aprendizaje en individuos que capturaron el mismo tipo de presa. El aprendizaje previo en el laboratorio, fue descartado, ya que se utilizó cada araña una única vez frente a cada presa. Sin embargo, las arañas podrían haber tenido experiencias con estas presas en el campo.

Considerando las diferencias en la captura de

presas con las diferencias de tamaño observadas por Robinson y Mirick (1971) y Japyassú y Ades (1990) y Uetz (1990) quién formuló la hipotésis que, la discriminación en algunas arañas de la familia Araneidae actúa sólo sobre el tamaño de la presa y no sobre la naturaleza de la misma, se descartó la influencia del factor tamaño, seleccionando presas de tamaño y peso homogéneo en relación a las arañas.

Bristowe (1941) usó tres especies de hormigas del género *Acanthomyrmex* como presas frente a 52 especies de arañas y comprobó que sólo diez especies las capturaron. Debido a sus caracteres defensivos (espinas, mandíbulas y ácido fórmico) la convierten en una presa peligrosa para un acercamiento directo. La peligrosidad de las hormigas condicionaría el no ser aceptadas fácilmente como presas para algunas arañas. *M. seditiosa* obtuvo un 100% de éxito en su captura,

Tabla 2.—Las variables utilizadas en la comparación fueron: latencia, duración total de la captura y número total de unidades. El test no refleja diferencias estadisticamente significativas.

	Tiempo de latencia		Duración total		No unidades	
	T	P	T	P	T	P
Acromyrmex	1.068	0.366	0.255	0.800	0.175	0.859
Musca	0.230	0.818	0.483	0.645	0.767	0.530

pero le implicó ataques de más duración y de mayor cantidad de componentes, demostrando una mayor cautela que ante *Musca* sp.

Eisner y Dean (1976) observaron que *Nephila* y *Argiope* frente a los escarabajos bombarderos realizaron Envolvimiento como primera unidad de la Fase de Inmovilización. Esta táctica de ataque coincidió con lo observado en *Metepeira seditiosa* frente a *Acromyrmex* sp. La elección de utilizar Envolvimiento como primera unidad en la táctica de ataque le permitiría a *Metepeira seditiosa* inmovilizar su presa y emponzoñarla sin riesgos, debido a que evita un contacto estrecho. Dicha táctica es usada sobre todas las presas que muerden, pican o esparcen fluídos nocivos cuando son atacadas (Robinson y Robinson 1981). La unidad con la que se inicia la Fase de Inmovilización de la presa (Mordeduras Cortas o Envolvimiento) indicaría la eficacia en la discriminación y la consiguiente táctica a utilizar.

Hays (1985) observó que la presa *Musca* sp. utiliza como táctica antipredadora permanecer en quietud, mientras la araña realiza la Fase de Detección y cuando el acercamiento de la araña es inminente, se debate violentamente, intentando soltarse de la red. Nuestras observaciones coincidieron con Hays (1985). El mecanismo defensivo utilizado por la mosca le permitiría confundirse con un objeto inmóvil.

Robinson y Robinson (1975) y Harwood (1974) en Araneidae y Ades et al. (1990) y Yoshida (1990) en Tetragnathidae han observado la utilización de la unidad Mordeduras Cortas como inicio del ataque. *Metepeira seditiosa* utilizó esta táctica frente a *Musca* sp., además de una mayor velocidad de respuesta observada en la captura. Este comportamiento resultaría adaptativo, debido al menor grado de adherencia de *Musca* sp. a la red, lo cual fue analizado por Eisner et al. (1964). Mediante la Fase de Detección la araña recibe información acerca del tipo de presa rápido e inofensivo, lo que precipitaría el ataque que se inició con Mordeduras Cortas. Robinson et al. (1969) observaron que *Argiope argentata* y *A. aemula* discriminaron entre varias presas utilizando la sucesión Mordedura - Envolvimiento para el ataque de presas relativamente inocuas pero rápidas para escapar, y la sucesión Envolvimiento - Mordeduras para presas peligrosas y fuertes. Dicha táctica, que favorece la discriminación de presas, fue observada asimismo en *Metepeira seditiosa*.

Suter (1978) constató que *Cyclosa turbinata* utiliza principalmente la sucesión Mordeduras - Envolvimiento. Posiblemente ésto se deba a la abundancia de presas rápidas e inofensivas en el hábitat de estas arañas, lo que determina que esta táctica resulte eficiente. El aspecto funcional de la unidad Envolvimiento fue tratado extensamente por Robinson et al. (1969) y Robinson y Robinson (1975), quienes afirmaron que la iniciación con Envolvimiento de la Fase de Inmovilización sería un carácter altamente evolucionado, presente en gran parte de la familia Araneidae. Las especies estudiadas cumplen una estrategia más especialista que *Metepeira seditiosa*. *M. seditiosa* es capaz de aceptar diferentes tipos de presas y capturarlas con éxito.

La alta correlación positiva entre el número de unidades de la Fase de Inmovilización y la duración de la misma, permitiría afirmar que el modelo de comportamiento de *Metepeira seditiosa* tiene un repertorio limitado de unidades, y que la complejidad de dicho comportamiento resulta del aumento en la frecuencia de las unidades y no de la duración de las mismas. La duración y la complejidad de la Fase de Inmovilización nos informa acerca de las dificultades que la araña tiene para capturar, dependiendo de las características de la presa.

La Fase Final fue la más estereotipada de las tres fases. Esta fase es menos importante para la discriminación, ya que las presas inmovilizadas no presentaron diferencias sustanciales entre sí. No se observó Transporte de las presas en los quelíceros y suponemos, de acuerdo con Robinson y Olazarri (1971), que se debió al tamaño relativamente grande de las presas. El Transporte en una pata serviría para mantener la presa alejada de la red cuando la araña se desplaza por ella (Robinson y Robinson 1970).

En trabajos de campo, Pasquet (1984) y Pasquet y Leborgne (1986, 1988) encontraron selección de presas en cinco especies de Araneidae. No pudimos comprobar en *M. seditiosa* si existió preferencia por alguna de las presas, debido a que el consumo de alimento en el laboratorio es frecuentemente más elevado que en el campo (Hagstrum 1970; Breymeyer y Jowik 1975).

El presente estudio mostró que *Metepeira seditiosa* posee una ampia gama de unidades de captura seleccionando la táctica depredadora adecuada para las diferentes tácticas defensivas ante *Musca* sp. y *Acromyrmex* sp., obteniendo un 100% de éxito de captura. Esta potencialidad depredadora de *Metepeira seditiosa* la señala como una especie potencialmente útil para el

control biológico de insectos de interés económico como dípteros vectores y hormigas cortadoras, éstas últimas plagas de la agricultura.

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AGRADECIMIENTOS

THE WEB AND BUILDING BEHAVIOR OF
SYNOTAXUS ECUADORENSIS (ARANEAE, SYNOTAXIDAE)

William G. Eberhard: Smithsonian Tropical Research Institute and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

ABSTRACT. Webs and building behavior of *Synotaxus ecuadorensis* are highly ordered and complex. Their webs differ from those of other *Synotaxus* species, but there are several apparent homologies in building behavior. The overall construction sequence differs from that of many other spiders in not being organized around a central portion or retreat. Instead, lines are added to one leading edge in a crochet-like fashion. Comparison with other *Synotaxus* species suggests how building behavior is organized within the spider.

RESUMEN. La tela y el proceso de construcción de la tela de *Synotaxus ecuadorensis* son complejas y altamente organizadas. La tela de esta especie difiere de las de otras especies de *Synotaxus*, pero el comportamiento de construcción muestra varias posibles homologías. La secuencia de pasos en la construcción difiere de muchas otras arañas en no estar organizada alrededor de un punto o area central. Al contrario, la araña agrega hilos al borde de la tela, en un proceso semejante a lo de la crochet. Se sugiere, a base de una comparición entre los comportamientos de las diferentes especies de *Synotaxus*, como esta organizada el comportamiento de construcción dentro de la araña.

Synotaxus is a small neotropical genus containing five described and at least one undescribed species (H. W. Levi, pers. comm.). A recent study suggests that this genus, which has traditionally been placed in the family Theridiidae, is part of a small group of genera (nearly all from New Zealand and Australia) that is the sister group of Nesticidae plus Theridiidae (Forster et al. 1990). The webs of two species, *S. turbinatus* Simon, and *Synotaxus* sp., include highly regular arrays of approximately vertical and horizontal sticky and non-sticky lines (Eberhard 1977). Webs are built as a series of approximately rectangular modules or "unit webs". Each unit begins with a pair of more or less parallel vertical, non-sticky lines. These are then joined by a series of more or less horizontal non-sticky lines, which are laid along with one to three zig-zag, sticky vertical lines in a complex series of events (Eberhard 1977).

Both the geometric design of the web and the construction behavior of the species of this study, *Synotaxus ecuadorensis* Exline, are simpler. The construction behavior is of special interest because it illustrates an overall building tactic (and thus a possible evolutionary route) which differs from that of many (perhaps most) other spiders, including those which make orbs (e. g., Foelix 1982; Eberhard 1990), those which make sheet webs, such as the theridiids *Latrodectus* spp.

(Szlep 1965; Lamoral 1968), the psechrid *Psechrus* sp. (Eberhard 1987), and the pholcid *Modisimus* sp. (Eberhard 1992; Eberhard & Briceño 1985), and those which make other centrally organized webs such as *Titanoeca albomaculata* (Szlep 1966) and *Filistata* spp. (Comstock 1948; Eberhard 1987, 1988). Instead of returning repeatedly to a central point during construction, *S. ecuadorensis* adds to its web by moving back and forth along one edge, gradually extending it in a manner analogous to crocheting.

METHODS

Observations were made between 25 June and 3 July 1992 in the Reserva Natural La Planada (elev. 1800 m), 8 km S. of Chuconés, Nariño, Colombia, in an area classified as montane wet forest in the Holdridgean system (Espinal & Montenegro 1963). Webs were in grassy second growth and early secondary forest. Twelve webs of eight different spiders (four of which were adult females) were observed. Most of the construction of two of these webs (both of adult females) was observed using the white light of a headlamp. Web initiation appeared to be inhibited by illuminating the spider, but once construction had begun the spider was apparently undisturbed by bright light. The use of bright light, plus the fact that spiders moved relatively slowly and used stereotyped movements which were frequently

repeated, made it possible to understand and record their actions in detail.

Voucher specimens of the spiders observed (numbers 3638, 3645, 3646) and mature males are deposited in the Museum of Comparative Zoology, Cambridge, Massachusetts 02138, USA.

RESULTS

Webs were built under long (>15 cm), more or less horizontal leaves. The upper portion of the web was a tangle of non-sticky lines attached to the underside of the leaf. The lines of the mesh were more closely spaced in the area where the spider rested during the day against the underside of the leaf. The spider's pale green color and its elongate abdomen, which it laid flat against the leaf, made it extremely cryptic. Egg sacs had thin walls with projecting processes, and the sphere of pale green eggs was plainly visible inside. The sacs (up to four per female) were suspended in the mesh under the leaf.

The approximately planar prey capture web, strung vertically below the mesh, varied to some extent (Fig. 1). The lateral edges of the capture web were formed by two long, more or less vertical, non-sticky "frame" lines. The interior portions contained more or less regularly spaced lines, most of which had many short (0.2–0.5 cm) segments of adhesive on them.

Initiation of capture web construction was not observed. Judging both by the lines present in the webs when first observed, and by the order in which subsequent lines were laid, it is probable that the first lines laid were the approximately vertical frame lines. One spider with only a mesh descended twice at the end of her dragline as if to begin construction early in the evening, but failed to contact a substrate below and climbed back up without making an attachment (and later abandoned the website).

Subsequent lines were added in a highly stereotyped order (Fig. 2). The spider began by attaching a dry line at the top of the capture web, usually near one edge. She then walked downward along the innermost line already present (this was the frame line in the first descent, and a line with adhesive segments in subsequent descents), attaching the non-sticky dragline she was laying periodically to the line along which she was walking (Fig. 2A). Immediately after each of these attachments, the spider backed up a short distance along the dragline and attached her dragline to it (Fig. 2A), thus making a short, more or less horizontal line (a "rung"), and then con-

tinued her descent. In one case the spider broke and replaced the distal portion of the frame line along which she was walking as she neared the bottom of the capture web.

After making the lowermost attachment to the line along which she was descending, the spider turned and began to climb the line she had just laid. She broke this line soon after she turned, and began reeling it up, replacing it with a new "sticky" line which consisted of a non-sticky line with evenly spaced short segments of sticky material. Each sticky segment was produced as both legs IV held the dragline and appeared to pull a short length from the spinnerets; the spider took one step forward with each leg IV (thus drawing out further silk), and then laid another sticky segment. Each time she reached a rung line, the spider broke it and performed a quick series of movements which I was unable to decipher, and then continued her upward climb. Judging by the pattern of lines when she was finished (Fig. 2B), probably the spider attached her dragline to the broken end of the rung line, paid out a short length of silk, and then attached her dragline to this line. A short segment of doubled line may have thus been produced, in a manner similar to the doubled lines laid during the descent (steps 2 and 3, and 4 and 5 in Fig. 2A). Each finished rung had a single spot of white near the middle, apparently corresponding to the broken end of the line to which the spider had attached her dragline.

In one web the spider alternated descents on the right and then the left side of the web. In another web she made several descents on one side (the larger of the two) before making any on the other. In both webs later lines with sticky material were progressively less vertical, as the spider filled in the central portion of the web (Fig. 2D). The final line was made following construction of the lowermost sticky line. The spider moved more or less directly upward through the middle of the capture web to the mesh above, laying a sticky line as she went. In one web the spider clearly broke all of the lines she encountered as she climbed, reattaching each to the sticky line she was laying. A short length of silk was paid out just before each reattachment, thus lowering the tension on these lines.

DISCUSSION

Although the prey capture webs of *S. ecuadorensis* are different from those of *S. turbinatus* and *S.* sp. (compare Figs. 1 and 2 with Fig. 3),
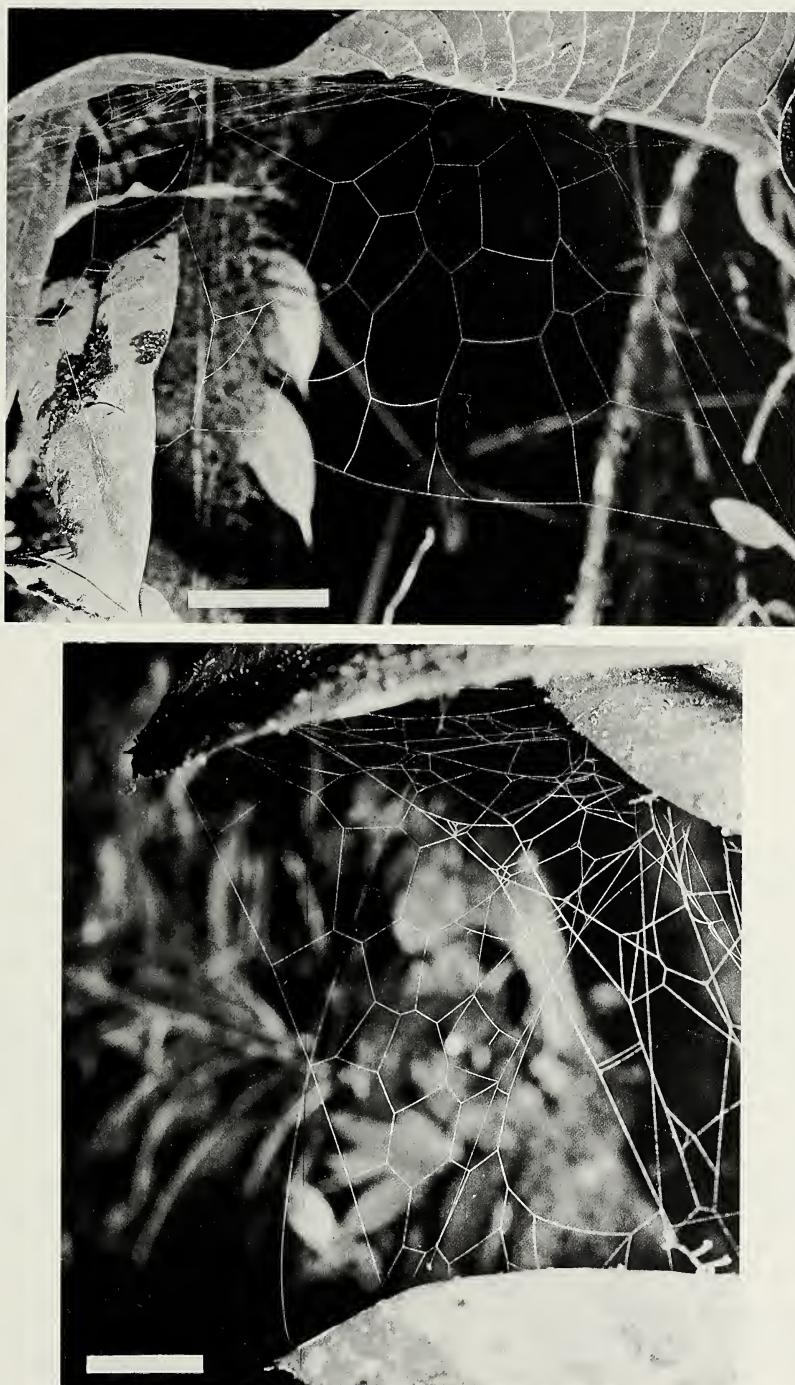
Figure 1.—Two newly-built capture webs of mature female *Synotaxus ecuadorensis* coated with cornstarch. The spider is just visible at the top of the upper web. In the lower web the lines at the right and the curved line from the tip of the leaf at the left are out of the plane of the capture web (scale lines = 5.0 and 6.0 cm for upper and lower webs).
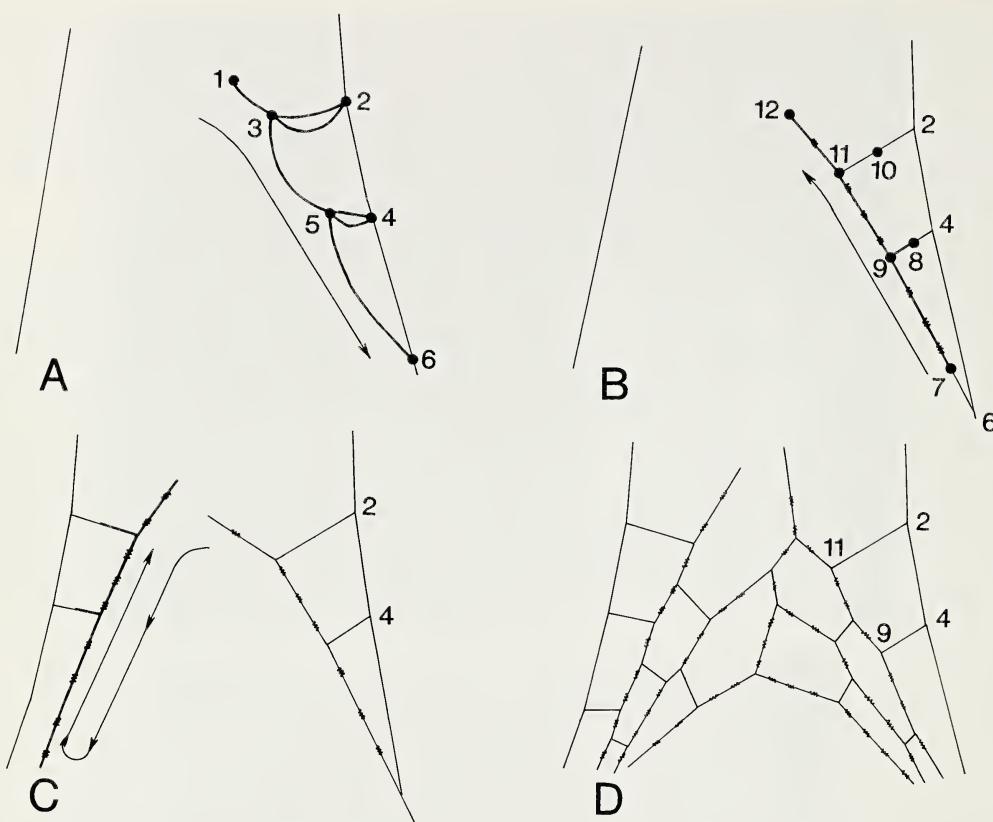
Figure 2.—Diagrammatic representation of the probable order of operations by *Synotaxus ecuadorensis* building a prey capture web. Thicker lines and large dots indicate the lines and attachments made during the period represented by each drawing; wiggly lines represent patches of adhesive; and numbers refer to the order of attachments. **A.** The spider starts from the mesh under the leaf along one of the two long non-sticky, more or less vertical lines that form the lateral borders of the web, laying a non-sticky dragline. Periodically she attaches the dragline to the frame (e. g., 2, 4), and backs up slightly and attaches to the line just laid (e. g., 3, 5) forming a "rung". She then continues downward to make a final attachment to the frame (e. g., 6). **B.** Turning back immediately, the spider breaks the line she has just laid, attaches her trail line to the broken end (7), and begins laying another line with sticky patches on it as she climbs back up along the line she just laid. She breaks each rung and attaches her dragline to the broken end (e. g., 8). Backing up slightly, she attaches to the line she just laid (e. g., 9) and continues upward, finally attaching the sticky line to the mesh near where she started (12). **C.** Subsequent lines are laid on the same or the opposite side of the web with a simIlar series of movements. **D.** Sticky lines laid later are progressively less vertical. The attachments 9 and 12 were deduced from the positions of lines in finished webs, while all others, and the breaking of lines at 7, 8 and 10 were confirmed by direct observations.

several details indicate that the prey capture web of *S. ecuadorensis* is homologous with a single "unit" of the web design of the others (Eberhard 1977) (Fig. 3). Both types of web are initiated with a pair of long, more or less vertical, straight, non-sticky lines which form their lateral margins. A complex sequence of behavior follows, in which construction of non-sticky and sticky lines alternate, with the sticky lines bearing widely spaced segments or dots of adhesive. One detail of this process in all three species is apparently unique

to *Synotaxus* among all araneoid web builders studied to date: after attaching its dragline to another line, the spider backs up a short distance and makes another attachment to the line it just laid, then continues onward (e. g., Fig. 2 A, B). A further similarity is that sticky lines are laid as the spider climbs upward, each replacing a non-sticky line laid during an immediately preceding descent. Construction ends with placement of a central sticky line laid as the spider ascends. Lines already present are apparently
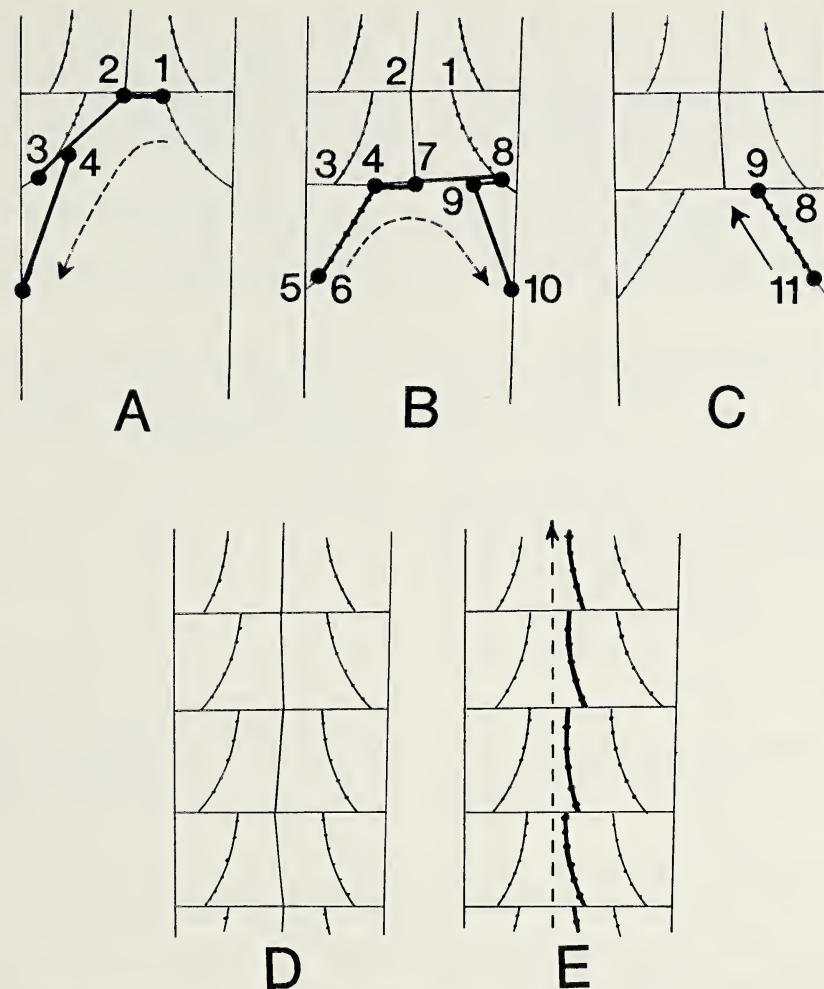
Figure 3.—Tentative order of operations in the construction of a unit web of *Synotaxus turbinatus* (after Eberhard 1977). The spider moves from side to side as she descends, laying both sticky and non-sticky lines (A, B, C). After reaching the bottom (D), she climbs up the middle of the web, replacing the non-sticky line with a sticky line (E).

broken and reattached to this central line. Both types of webs are vertical, more or less planar, and relatively fragile arrays that are rebuilt daily, and are located immediately below a more permanent mesh of non-sticky lines near the underside of a large leaf where the spider rests. These proposed homologies must remain tentative, however, until further data on *Synotaxus* and related genera become available. The apparent homology of the *S. ecuadorensis* web to a unit of the webs of other *Synotaxus* species indicates that the "units" of these species are not simply abstractions, but that web construction may be also organized in the spider's nervous system as units.

Differences between the webs and construction behavior of *S. ecuadorensis* and that of other *Synotaxus* are also substantial. They include the following: the web is constructed as a single unit, with only a single pair of vertical frame lines rather than as a series of modules; a long, uninterrupted non-sticky line is laid during each descent and is nearly completely removed during the ensuing ascent; placement of adhesive material is in short segments rather than single balls on the sticky lines; and there is no non-sticky "frame" line at the bottom of the web (also sometimes lacking in other *Synotaxus*).

The construction behavior of *S. ecuadorensis* is to my knowledge the clearest described ex-

ample in which a spider does not organize its activities around a central area. Instead, after establishing three sides of the planar web (the mesh above and the two lateral frames), the spider moves back and forth across the fourth side, gradually extending the web in a process analogous to crocheting. I have seen a similar process only one other spider (a species of the theridiid *Chrosiothes* which repairs holes in its sheet in this manner) (Eberhard, pers. obs.).

ACKNOWLEDGMENTS

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LOS NERVIOS OPTICOS EN CUATRO ESPECIES DE
LACTRODECTUS (ARANEAE, THERIDIIDAE)

Carmen J. de la Serna de Esteban y **C. Mónica Spinelli:** Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Departamento de Ciencias Biológicas. Ciudad Universitaria Pabellón II 4 Piso Lab. 22- (1428) Buenos Aires, Argentina

ABSTRACT. The pathway of the optic nerves in the studied species of *Latrodectus* shows intraspecific variation. Dilatations, empty or containing a pigment of unknown function, can be seen in the nerves. Curiously, this pigment originates in the retinal cells. The optic nerves run through the prosoma and merge, forming two or four optic centers, which are finally joined into a single one.

RESUMEN. La trayectoria de los nervios ópticos en las especies de *Latrodectus* estudiadas muestra variación intraespecífica. En ellos existen dilataciones que pueden hallarse vacías o conteniendo un pigmento originado en las células retinianas, cuya función es desconocida. Estos nervios forman dos o cuatro centros ópticos que luego se fusionan en un centro único.

El trayecto de los nervios ópticos en el prosoma de varias especies de *Tegenaria* Latreille 1804 fue estudiado por Legendre (1959), quien sin determinar el ordenamiento de los mismos confirmó que este género carecía de quiasma óptico. Este autor dice que los nervios ópticos surgen de la superficie anterior del ganglio cerebroide, hallándose constituído cada uno de ellos por tres haces de fibras, los que se dirigen a los ojos laterales, y por encima de los cuales se encuentra un pequeño haz impar. El mismo autor, halló estas mismas particularidades con mínimas variaciones en especies que no cita en el trabajo, así como tampoco las familias sobre las que realizó el estudio.

Homann (1947) considera que en la araña sedentaria *Araneus sexpunctatus*, los nervios ópticos penetran en conjunto en el ganglio cerebroide, originándose así un centro óptico único.

Baccetti y Bedini (1964) realizaron estudios mediante microscopía óptica y electrónica en los ojos de *Arctosa variana* (Lycosidae), en los que señalan la presencia de un pigmento claro en los nervios ópticos, sin especificar origen ni naturaleza química del mismo.

En el presente trabajo se estudió el recorrido de los nervios ópticos en el prosoma, en cuatro especies del género *Latrodectus* (Araneae, Theridiidae) obteniéndose resultados que no coinciden con las observaciones realizadas para otras especies, por los mencionados autores.

Por otra parte el llamativo recorrido de los nervios ópticos, con variaciones intraespecíficas condujo a realizar un estudio comparativo de los mismos.

METODOS

Se emplearon 11 ejemplares del género *Latrodectus*: dos individuos de *L. geometricus* Koch 1841, dos de *L. mirabilis* Holmberg 1876, cuatro de *L. antheratus* Badcock 1932 y tres de *L. corallinus* Abalos 1953.

Los fijadores utilizados fueron: formol 10%, Helly y Bouin y la inclusión se realizó en parafina. Las coloraciones histológicas de rutina fueron: Hematoxilina de Carazzi - Ponceau de Xilidina - Azul de Anilina, Mallory - Heidenhain (Azan), fucsina paraldehída según Gabe (Martoja y Martoja Pierson). Las coloraciones histoquímicas fueron: Periodic Acid Schiff (P. A. S), coloración para proteínas según Martoja y Alcian Blue a diferentes pH.

Para la indentificación de los nervios ópticos correspondientes a cada ojo, en su trayectoria, se confeccionaron esquemas rotulándose los nervios con las siguientes abreviaturas: OMA: ojo medio anterior; OLA: ojo lateral anterior; OMP: ojo medio posterior; y OLP: ojo lateral posterior.

Dado que los nervios se fusionan de a pares a corta distancia de su emergencia del ojo, se ha empleado la siguiente denominación. n_1 = OMA derecho + OLA derecho; n_2 = OMA izquierdo
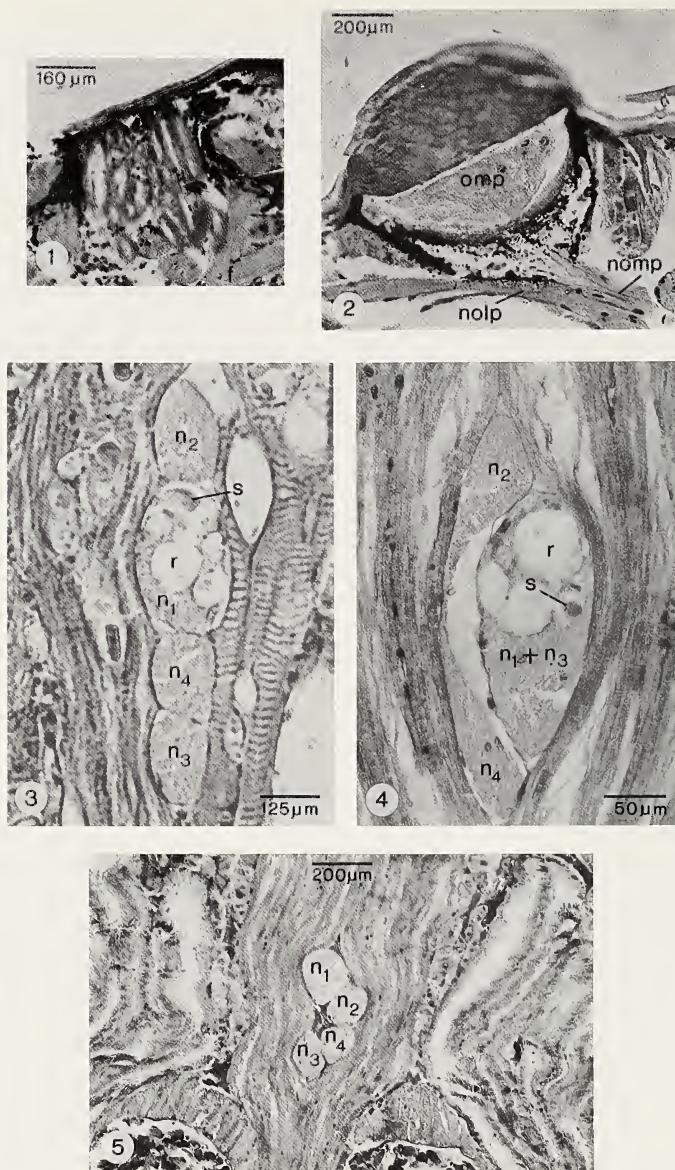
Figuras 1–5.—Nervios en especies de *Latrodectus*. 1, *Latrodectus mirabilis* – fusión del nervio del ojo medio posterior con el del ojo lateral anterior (f); 2, *Latrodectus geometricus* – fusión del nervio del ojo medio posterior con el del ojo lateral posterior, nomp = nervio del ojo medio posterior, nolp = nervio del ojo lateral posterior, omp = ojo medio posterior; 3, *Latrodectus mirabilis* – Corte de la zona anterior del prosoma con los cuatro nervios ópticos en la línea media, en n1 se observan axones dilatados y vacíos, excepto uno superior que contiene restos de la secreción originada en el ojo, r = dilatación del nervio, s = restos de secreción; 4, *Latrodectus mirabilis* – Principio de fusión de $n_2 + n_4$, y $n_1 + n_3$ ya fusionados, r = dilatación del nervio o reservorio vacío, s = restos de secreción; 5, *Latrodectus corallinus* – $n_1 + n_2$ y $n_3 + n_4$ antes del punto de fusión

+ OLA izquierdo; n_3 = OMP derecho + OLP derecho; n_4 = OMP izquierdo + OLP izquierdo.

Para apreciar las variaciones en la ordenación de estos nervios fusionados, se han considerado en el Cuadro I tres regiones representativas del prosoma: una zona anterior, una zona media y una posterior. En la zona anterior, donde los nervios se disponen en forma vertical, se han asignado las letras A, B, C y D a los diferentes tipos de disposición, siendo: Tipo A = n_1, n_2, n_3,
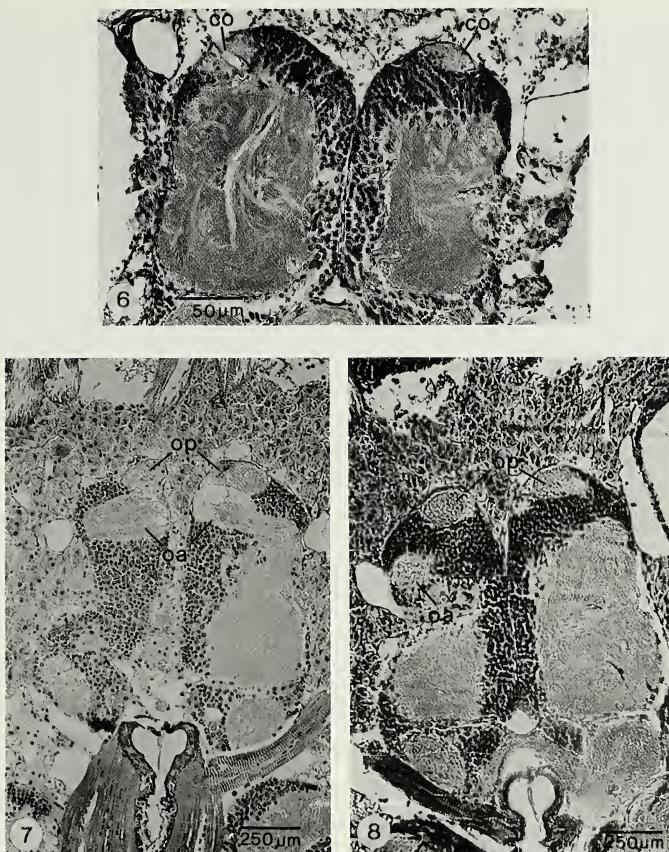
Figuras 6–8.—Los centros opticos de especies de *Latrodectus*. 6, *Latrodectus corallinus* – Dos centros ópticos (co) en el ganglio cerebroide; 7, *Latrodectus geometricus* – Cuatro centros ópticos en el ganglio cerebroide, ca = centro óptico de los ojos anteriores, op = centro óptico de los ojos posteriores; 8, *Latrodectus geometricus* – En un corte transversal en vista anterior se observan dos centros ópticos del lado derecho. En el lado izquierdo se observa solo uno, debido a la fusión del centro óptico de los ojos anteriores, con el de los posteriores del mismo lado, ca = centro óptico de los ojos anteriores, op = centro óptico de los ojos posteriores.

n_4; Tipo B = n_1, n_2, n_4, n_3; Tipo C = n_2, n_1, n_3, n_4; Tipo D = n_2, n_1, n_4, n_3.

OBSERVACIONES

En el género *Latrodectus* se observaron sólo cuatro nervios ópticos en la línea media del prosoma (Figs. 3, 5). Esto se debe a que el nervio de cada ojo medio anterior se fusiona con el nervio del ojo lateral anterior del mismo lado en un punto cercano a la salida del ojo. Idéntica disposición se observa en los ojos posteriores (Figs. 1, 2).

De los resultados volcados en el Cuadro I surge que en la zona anterior del prosoma, hay una ordenación variable en la trayectoria de los nervios en cada especie estudiada y aún entre individuos de la misma especie.

En el trayecto prosomático (zona media), se produce una nueva ordenación y fusión de los nervios ópticos uniéndose de la siguiente forma: a) Todos los nervios correspondientes a los ojos anteriores (medios y laterales) del lado derecho, con todos los nervios de los ojos posteriores (medios y laterales) del mismo lado. b) Todos los nervios de los ojos anteriores y posteriores del lado derecho y a su vez, todos los nervios anteriores y posteriores del lado izquierdo. En el caso a) penetran en primer término los nervios correspondientes a los ojos posteriores y luego los correspondientes a los ojos anteriores. Dando origen a cuatro centros ópticos, dos en cada lado (Figs. 7, 8). En el caso b) se forman sólo dos centros ópticos, uno de cada lado (Fig. 6). En ambos casos los centros ópticos se fusionan entre
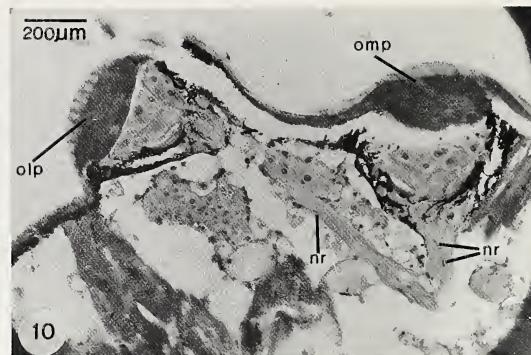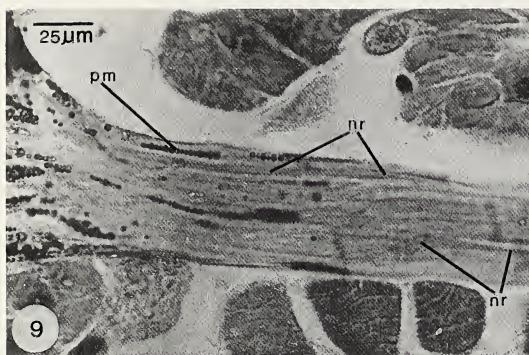
Figuras 9–10.—*Latrodectus geometricus* – Neurosecreción retinal en el nervio óptico del ojo lateral posterior. pm = pigmento melánico, nr = neurosecreción retinal; 10, *Latrodectus corallinus* – omp = ojo medio posterior, olp = ojo lateral posterior, nr = nervios con neurosecreción retinal.

sí con posterioridad, formando un centro óptico único.

Estudiando diversos preparados coloreados con las técnicas habituales, se observó el pigmento amarillo - anaranjado detectado ya por Bacetti y Bedini (1964). Este pigmento es muy evidente dentro de los axones que constituyen los nervios ópticos (Figs. 3, 4, 9, 10) pero nunca se presenta en los centros ópticos del ganglio cerebroide. Antes de alcanzar el centro óptico el pigmento ha desaparecido, quedando en los axones de los nervios óptico dilataciones muy llamativas, vacías o con restos de secreción (Figs. 3, 4).

DISCUSION

Las observaciones realizadas coinciden con la afirmación de Legendre (1959) sobre la ausencia de quiasma óptico. Este autor señala la presencia de ocho nervios ópticos en la línea media del prosoma en dos especies del género *Tegenaria*, y sostiene que su origen se halla en el ganglio cerebroide, lo cual no ocurre en las especies estudiadas del género *Latrodectus*.

Las fibras o axones que constituyen los nervios ópticos son puramente sensoriales y forman un neuropilo óptico donde según Trujillo-Cenoz (1965) sinaptan células visuales ganglionares. Por otra parte, en las especies estudiadas, la precoz fusión de los nervios ópticos reduce su número a cuatro, sin que ello signifique por ejemplo, que exista alguna relación entre esa reducción y el tipo de tela que la araña construye.

Homann (1947) halla en la familia Theriididae un centro óptico único en el ganglio cerebroide. El género *Latrodectus* pertenece a la misma familia, y en las especies de este género estudiadas en el presente trabajo, se comprobó que en la zona anterior del ganglio cerebroide, se pueden encontrar dos o cuatro centros ópticos según el tipo de fusión de los nervios ópticos, los que a su vez se fusionan formando un centro óptico único.

Heinrichs y Fleissner (1987) observan la presencia de neurosecreción llamada precerebral en la retina de los ojos medios, proveniente de neuronas centrales y relacionada con información circadiana, en el escorpión *Androctonus australis*. En este caso la neurosecreción tiene su origen en neuronas cerebrales ubicadas en el ganglio cerebroide, y es llamada precerebral por estar dirigida hacia los ojos. No es este el caso de *Latrodectus*, pues la neurosecreción se origina en neuronas sensoriales (células retinales) situadas por supuesto por delante del ganglio cerebroide.

Con el fin de no confundir conceptos se ha optado en este caso por denominarla "neurosecreción retinal".

Las dilataciones axonales corresponderían a sitios de almacenamiento de la secreción proveniente de las células retinales, y la naturaleza química de la misma no ha podido determinarse con exactitud mediante las técnicas histoquímicas empleadas aunque puede sospecharse que se trata de una sustancia proteica dado el color amarillo que presenta en preparados coloreados con la técnica para proteínas de Martoja-Martoja.

Estos resultados estarían apoyados por el hecho de que las hormonas elaboradas por neuronas, que son células de origen ectodérmico, son polipéptidos. Esta reflexión conduce a desechar la posibilidad de que se trate de esteroides, puesto que los mismos son producidos por tejidos de origen mesodérmico.

Cuadro 1.—Esquema de las diversas disposiciones observadas en corte transversal de los nervios ópticos en cuatro especies de *Latrodectus,* en la región cercana a la línea media o mediana del prosoma, y considerando las tres zonas antes indicadas. Las posiciones relatívas de los números dentro de cada casillero, indican la ordenación espacial de los nervios ópticos. (El tipo de disposición A puede verse en la Fig. 5, y el tipo B en la Fig. 3.)

	Tipo de disposición	Zona anterior	Zona intermedia	Zona próxima a los centros ópticos	
Latrodectus geometricus	A	1	2	1	2
		2	1		
		4	4	3	4
		3	3		
	B	2	2	1	2
		1	1		
		4	4	3	4
		3	3		
Latrodectus mirabilis	C	2	2	1	2
		1	1		
		3	3	3	4
		4	4		
	B	2	2	1	2
		1	1		
		4	4	3	4
		3	3		
Latrodectus antheratus	D	1	2	1	2
		2	1		
		3	4	3	4
		4	3		
	A	1	1	1	2
		2	2		
		4	4	3	4
		3	3		
	C	2	1	1	2
		1	2		
		3	4	3	4
		4	3		
	B	2	2	1	2
		1	1		
		4	4	3	4
		3	3		
Latrodectus corallinus	D	1	1	1	2
		2	2		
		3	3	3	4
		4	4		
	A	1	1	1	2
		2	2		
		4	4	3	4
		3	3		
	B	2	2	1	2
		1	1		
		4	4	3	4
		3	3		

CONCLUSIONES

Resumiendo lo observado en los preparados y los datos consignados en el Cuadro I, se puede afirmar que: 1. No existe quiasma óptico. 2. En las cuatro especies estudiadas (*Latrodectus mirabilis, L. antheratus, L. corallinus* y *L. geometricus*) el nervio óptico de cada ojo medio se fusiona con su lateral correspondiente en la zona anterior del prosoma. 3. Dentro de cada una de las especies estudiadas, los nervios no presentan una disposición constante en su trayecto a través del prosoma. 4. En la zona media del prosoma, donde se produce la segunda fusión de nervios se mantiene el siguiente esquema, a) si la fusión se realiza entre los nervios de los ojos medios y laterales anteriores de ambos lados y los de los ojos medios y laterales posteriores también de ambos lados dan origen a cuatro centros ópticos (dos de cada lado) ubicados en la región anterior del ganglio cerebroide, y b) si la fusion se produce entre los nervios de los ojos anteriores (medios y laterales) con los de los ojos posteriores (medios y laterales) del mismo lado originan sólo dos centros ópticos, ubicados también en la región anterior del ganglio cerebroide. 5. En la región posterior del ganglio cerebroide, los centros ópticos se fusionan, cualquiera sea su número (dos o cuatro) en un centro óptico único. 6. En el presente trabajo se considera que los nervios ópticos están constituídos por axones de las células retinales y no de las neuronas que constituyen el ganglio cerebroide. 7. En las células retinales del ojo se produce una neurosecreción que se desplaza por dentro de los axones de los nervios ópticos y es eliminada antes de ingresar en los centros ópticos del ganglio cerebroide. A dicha secreción se la ha denominado "neurosecreción retinal".

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DIRECT EVIDENCE FOR TRADE-OFFS BETWEEN FORAGING AND GROWTH IN A JUVENILE SPIDER

Linden E. Higgins: Dept. of Zoology, University of Texas at Austin, Austin, Texas 78712 USA

ABSTRACT.   A simple modification of classical optimal foraging models yields explicit predictions of the allocation of resources to orb-web synthesis and weight gain in a spider. Because the spiders may be trying to avoid weight loss, weight gain and web size are predicted to be be negatively correlated at higher food levels and positively correlated at lower food levels. These predictions were upheld qualitatively by experiments involving juvenile *Nephila clavipes* and *N. maculata*.

RESUMEN.   Una sincilla modificación a los modelos clásicos del forrajeo óptimo da predicciones explícitas sobre la repartición de recursos entre el sintesis de la tela orbicular y el aumento de peso en una araña. Dado que arañas posiblemente están ententando evitar la pérdida de peso, la interacción entre el aumento de peso y el tamaño de la tela deberia estar negativamente correlacionada bajo majores niveles de alimentación, y positivamente correlacionada bajo de condiciones de alimentación reducida. Estas predicciones fueron appoyadas experimentalmente utilizando juveniles de *Nephila clavipes* y *N. maculata*.

Classical foraging models are based on the assumption that optimal allocation of limiting resources among various expenditures increases the fitness of the organism either directly (through increased reproductive success) or indirectly (through increased growth) (e. g., Schoener 1971; Pyke et al. 1977; Mangel & Clark 1986). Despite the key role of this assumption, few studies have described the interaction between foraging investment and growth at different levels of food availability. This appears in part due to the difficulty of finding common units of measure (Pianka 1981; Stephens & Krebs 1986). If common resources are used for both growth and foraging, then explicit predictions can be made concerning their allocation at different levels of prey availability.

The study of foraging in orb-web building spiders allows observation of resource allocation because foraging investment is measurable as material investment into the web, and the orb is composed of physiologically important compounds. The orb web is renewed regularly, and changes in orb-web size reflect the response of the spider to foraging conditions (Buskirk 1975; Gillespie 1987; Higgins & Buskirk 1992). The viscid silk that forms the spiral of the orb is a protein thread coated with a mixture of organic compounds that also have physiological functions (Tillinghast 1984; Dadd 1985; Townley et al. 1991). Thus, construction of each orb requires decisions concerning the allocation of metabolically important compounds; such decisions could directly affect growth.

In some large araneoid spiders, fitness is increased by rapid development and weight loss is predicted to reduce the fitness of the females (Higgins & Rankin, in press). The existence of resources common to both foraging and growth and the fitness penalties associated with weight loss imply that when resources are limiting, foraging behavior might be different from that predicted by foraging models calculating maximization of the rate of energy intake. Here, I present a simple model that predicts patterns of allocation of resources between foraging and weight gain at food levels varying from very low to very high. I experimentally tested this model using juvenile *Nephila clavipes* (L.) and *N. maculata* (Fabr.) (Araneae: Tetragnathidae) that were fed at very low, intermediate and high levels.

THE MODEL

If it is true that the functions of weight gain and web building are competing for common resources and if it is important to the individual to avoid weight loss, a simple modification of the classic foraging investment models (Schoener 1971) is necessary to predict behavior at very low levels of prey availability. The model is pre-
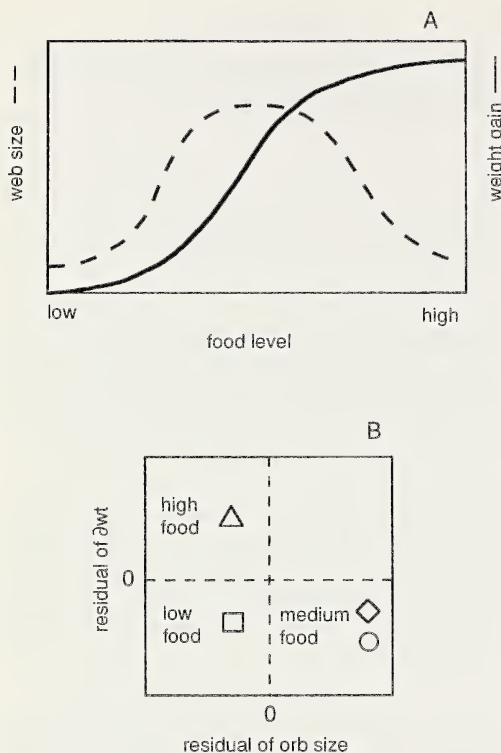
Figure 1.—The model of resource allocation by an orb-weaving spider. **A.** As food resources increase for a given individual, orb size increases then declines and weight gain increases. **B.** Among spiders, the residuals of orb size and weight gain regressed against spider size are compared (eliminating the variation due to spider size). At low food levels (square), orb size and weight gain are lower than average; at medium food levels (circle, diamond), orb size is greater and weight gain is lower than average; and at high food levels (triangle), orb size is lower and weight gain is higher than average.

sented graphically in Fig. 1. At high to intermediate levels of food, the spiders have sufficient resources to avoid weight loss and increase investment into foraging as food levels decrease. This is consistent with classical foraging models: as average foraging success decreases, the investment into hunting (e. g., searching time per patch) is predicted to increase (maximizing energy gain/effort; Stephens & Krebs 1986). If common resources are being allocated into growth and foraging then the rate of weight gain will be slower, due to both decreased prey capture and increased foraging investment. However, this prediction will not hold at lower food levels if the spiders must avoid weight loss. When resources are so limiting that weight loss would be the price of continued increases in foraging in-

vestment, the spiders should reduce their foraging effort. Thus, the relationship between weight gain and web investment in spiders is predicted to be negatively correlated at higher food levels, and positively correlated lower food levels.

METHODS

In order to test the prediction that the relative investment into the orb and weight gain will differ between the shift from very low to intermediate foraging success and the shift from intermediate to high foraging success, I controlled prey availability in juveniles of two species of *Nephila*: lab-reared *N. clavipes* in Panama and field-collected *N. maculata* in Madang, Papua New Guinea. In both cases the investment into weight gain and orb area were recorded as functions of prey availability, measured as the daily prey weight/initial spider weight.

The basic methods were the same in the two experiments. To control the structural environment used in web construction, I placed individuals on 30 cm diameter spherical frames consisting of two hoops of 3 mm × 6 mm fiberglass, fixed at right angles and suspended from the ceiling or braces in open-air insectaries. I fed spiders locally available stingless bees (*Trigona* sp.), a common prey item of these spiders (Higgins & Buskirk 1992; Higgins, pers. obs.). Bees were collected from the same nests throughout the experiment.

For each animal, I recorded daily orb-web area and rate of weight gain. (Mesh size, measured as the number of spiral strands per 2 cm (Higgins & Buskirk 1992), did not vary with food level in either species. *N. clavipes*: $F_{(1, 34)} = 3.16$, *ns*; *N. maculata*: $F_{(2, 13)} = 0.34$, *ns*). Orbs built by these spiders are asymmetrical, and orb-web area was estimated as a half ellipse using measurements of the vertical and horizontal radii. While many orb weavers replace the orb each day, these spiders sometimes only partially renew the orb (Lubin 1973). When a web was partially new, the area was estimated by calculating the area of the orb then reducing to the estimated area that was new ($\leq \frac{1}{3}$, $\leq \frac{1}{2}$, $\leq \frac{2}{3}$, $\leq \frac{3}{4}$). Orbs are not of constant size during the intermolt interval (Higgins 1990), therefore, foraging investment was measured as the mean area of all orbs spun during the intermolt period. If a spider did not molt during the experiment, the mean area during the experiment was used.

Web size and rate of weight gain are both functions of spider size. Spider size was measured as
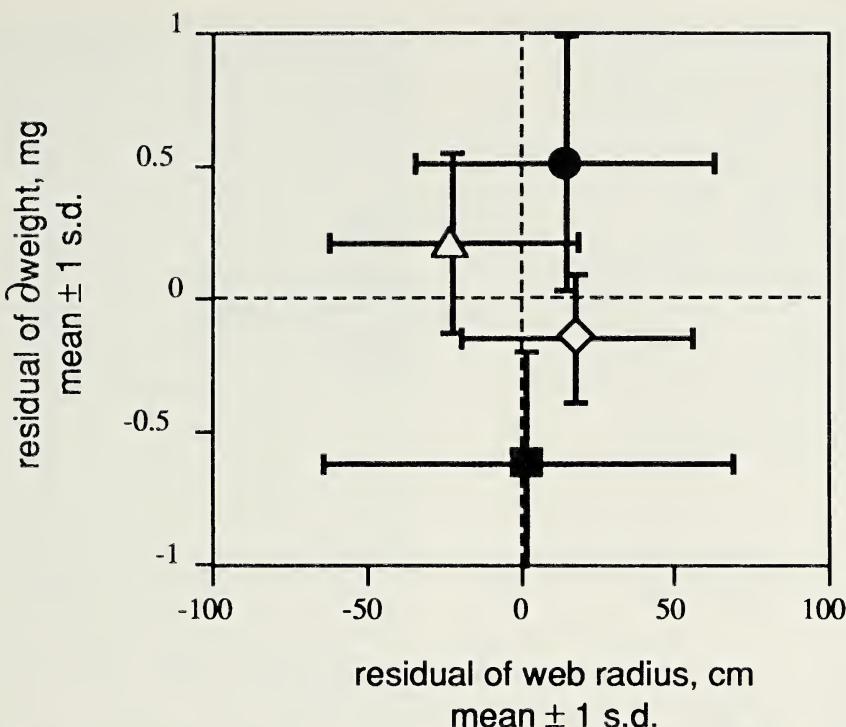
Figure 2.—The relationship between mean orb-web size and mean daily weight gain in *Nephila clavipes* under three different food levels (% initial spider weight), two trials. Trial 1 (filled symbols): diamond – 20%, triangle – 35%. Trial 2 (open symbols): square – 10%, circle – 20%.

the length of the leg I tibia + patella length, cm (TPL), which does not vary between molts. Spider weight, which increases between molts, can be estimated from TPL and abdomen volume (Higgins 1992a; the same equation was used for both species). The rate of weight gain in mg was calculated for all spiders as δwt mg (= wt_{Final} − $\delta wt_{Initial}$/no. days observed). To eliminate the influence of size, the residuals of web size and weight gain regressed against spider size were the dependent variables in the statistical analyses. Multivariate analysis of variance (MANOVA) allowed simultaneous comparison of the effects of prey level on the rate of weight gain and web size. When the MANOVA was significant, as indicated by Wilks' lambda, ANOVA were used to examine the variation in each dependent variable.

Nephila clavipes.—For this experiment, I raised spiders from both generations of a bivoltine population on Barro Colorado Island, Panama. First-generation females mature in the early rainy season (May-June), and second generation females mature as the rains end (December-January) (Higgins 1992a). Eggs were collected from two

gravid females of each generation. The first two cohorts of spiderlings hatched in January, and the second two cohorts hatched in May of 1986, resulting in two separate trials. Each cohort was kept in a fine-screened cage (15 cm w. × 30 cm l. × 60 cm h.) within an open-air, screened insectary, and large numbers of field-caught *Drosophila* spp. were released into the cages twice daily. As each spider reached the third instar, it was removed from the common cage, marked and placed onto a spherical frame. During this instar, each spider was offered one stingless bee daily (mean weight 3.5 mg, mean body length 4 mm).

The experimental treatment was initiated in either the fourth (first trial) or fifth (second trial) instar. Within each trial, the spiders were fed either two or one stingless bees daily, the mean number of prey captured per day in the field in the rainy and dry seasons, respectively (Higgins & Buskirk 1992). As each spider molted, it was measured (TPL, abdomen length and width, cm), individually marked with Testors® enamel paint, and randomly assigned to receive one or two bees/day. Penultimate-instar males may parti-
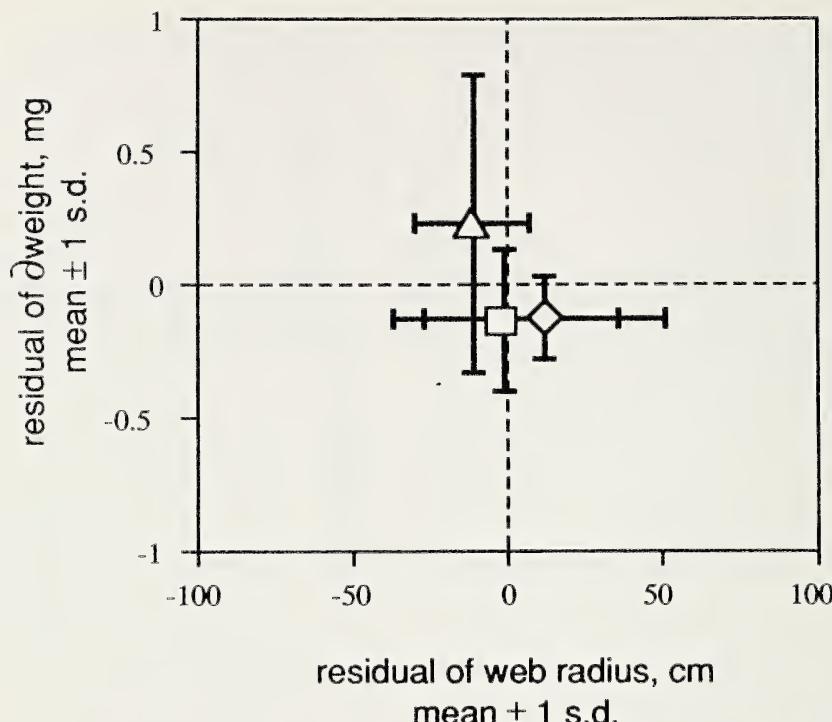
Figure 3.—The relationship between mean orb-web size and mean daily weight gain in *Nephila maculata* under three different relative food levels (% initial spider weight). square: <17%; triangle: <22%; diamond: <45%.

tion resources differently (Higgins 1993); therefore, males in this instar were not used in the experiments. Treatment lasted 14 days, slightly longer than the mean intermolt interval of the fourth instar. If, at any time, an individual moved off its frame, the support strands of the new web were carefully cut and the spider with its web was placed back onto the frame, after measurements (after M. Robinson, pers. comm.). Movement off of the frames occurred with equivalent frequency in all groups (test for full independence: $G = 6.61$, $df = 4$, *ns*; Sokal & Rohlf 1981).

The experimental treatment was started on average one instar later in the second trial. Because of the difference in instar between the two trials, the spiders differed in initial size and weight. Therefore, the two treatments (1 *vs.* 2 prey/day) yielded three levels of prey weight relative to initial spider weight: high (35%) and medium (20%) in the first trial, medium (20%) and low (10%) in the second. One individual's relative food weight was 26%; preliminary analyses indicated no difference in the statistical outcome when it was included in the medium or high group, so it was assigned to the former.

The regressions of orb area and rate of weight gain against spider size were significant (orb area $= 166.6 + 521.6$ (TPL); $R^2 = 0.57$, $F_{(1,36)} = 48.81$, $P < 0.001$; ln(δwt) $= -1.82 + 2.80$ (TPL), $R^2 = 0.09$, $F_{(1,34)} = 3.53$, *ns*). Insufficient spiders survived to allow examination of variation among clutches, but the spiders of both clutches were assigned to each treatment within a trial, controlling for this factor.

Nephila maculata.—In February and March of 1993, I conducted a similar experiment with *N. maculata*. Small groups (no more than 10 at a time) of second -- fifth instar spiders from the forests of Baitabag village, west of Madang, Papua New Guinea, were held indoors overnight to encourage building on the frames. Afterwards, the spiders were moved to a screened, roofed insectary, and randomly assigned to a diet (low or high). The number of prey items was adjusted according to spider instar. I fed second and third instar spiders *Drosophila* spp.(0.67 mg each; low = 2/day, high = 4/day (second instar) or 6/day (third instar)), and larger spiders *Trigona* bees (5 mg each; low = 1/day, high = 2/day). The experimental treatment was continued for 10 days,

after which the spiders were returned to the forest and new individuals were collected. The shorter interval reflects both the shorter intermolt duration of this species, and the need to maximize the number of animals used in the experiment. Although I had randomly assigned prey availability, I could not make the spiders eat and prey consumption was highly variable. Therefore, the independent variable used in the statistical analyses is the relative mean weight of prey actually eaten (presented as % initial spider weight). The continuous distribution of prey consumed was divided into three approximately equal groups of increasing relative prey weight.

N. maculata were not as likely as N. clavipes to build an orb each day, perhaps due to the insectary being roofed. Therefore, the foraging investment reported is the total area of orb built during the experiment divided by the number of days hunting (determined as the number of days with a new orb plus the number of days that the spiders accepted prey although a new orb had not been built). The size range of spiders used was larger than in the previous experiment, so the data had to be transformed to correct for heteroscedasticity prior to statistical analysis of the residuals (ln (δwt) = $-0.997 + 2.698$ (TPL), $R^2 = 0.33$, $F_{(1,15)} = 7.398$, $P < 0.025$; (web/hunt)$^{1/2}$ $= 8.506 + 10.67$ (TPL), $R^2 = 0.34$, $F_{(1,15)} = 8.26$, $P < 0.025$).

RESULTS

Nephila clavipes.—Both rate of weight gain (δwt) and mean orb size varied with food level (Fig. 2). From 10% to 20% relative food (second trial), δwt and orb size increased, while from 20% to 35% relative food (first trial), δwt increased and orb size decreased. Three MANOVA compared the responses of the spiders to food level within each trial, and compared between trials at the 20% food level; the significance levels were adjusted for multiple, non-independent tests. In the second trial, there was a significant effect of food level on δwt but not on web size (Wilks' λ = 0.356, $P < 0.01$; ANOVA: δwt: $F_{(1, 13)}$ = 23.5, $P < 0.001$; web size: $F_{(1, 13)}$ = 0.20, ns). There was a significant effect in the first trial on both web size and δwt (Wilks' λ = 0.568, $P < 0.01$; ANOVA: δwt: $F_{(1, 19)}$ = 8.09, $P = 0.01$; web size: $F_{(1, 19)}$ = 5.41, $P = 0.03$). Between trials, there was a significant difference in δwt but not web size (Wilks' λ = 0.514, $P < 0.01$; ANOVA δwt: $F_{(1, 17)}$ = 16.05, $P < 0.01$; web size: $F_{(1, 17)}$ = 0.03, ns). The effect of trial in the medium food level
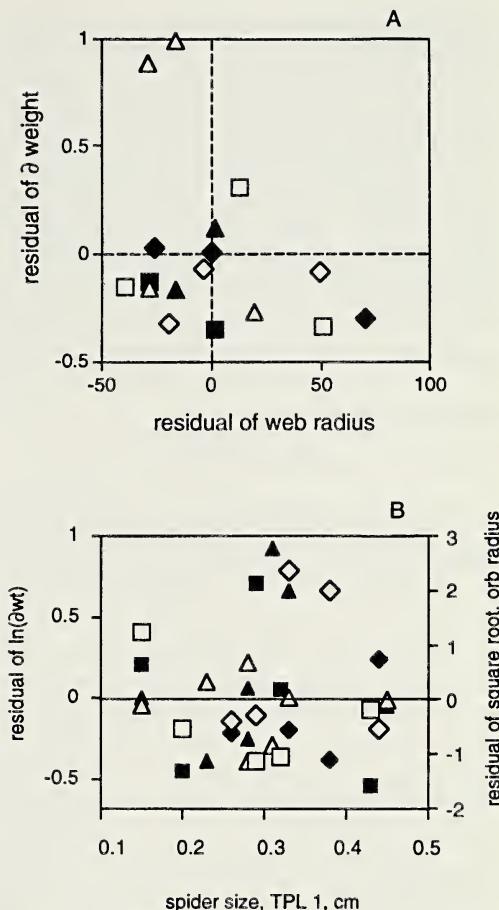
Figure 4.—The relationship between mean orb-web size and mean daily weight gain in individual *Nephila maculata* under three different food levels (% initial spider weight). Square – <17%, triangle – <22%, diamond– <45%. **A.** There is no effect of the sex of the individual on resource allocation. Male = filled symbols, female = open symbols. **B.** There is no effect of initial spider size on resource allocation. Filled symbols = residual of orb-web size, open symbols = residual of δwt.

is probably due to the larger mean initial spider size in trial 2.

Reduced rate of weight gain had a significant negative effect on the development rate of the spiders, observed as an increase in the number of days between molts. Eighteen spiders from trial 1 were held on the assigned diet until they molted and the number of days between molts was correlated with the rate of weight gain and initial spider size (ln (days between molts) = 1.96 $- 37.7$ (δwt) + 4.81 (TPL); $R^2 = 0.46$, $F_{(2, 15)} =$ 6.25, $P = 0.011$; only 5 spiders molted in trial 2).

Nephila maculata.—Although the pattern of variation in orb investment and rate of weight gain among the three groups is similar to that observed for *N. clavipes*, the differences are not significant (Fig. 3; Wilks' $\lambda = 0.78$, $P = 0.5$). What is most striking is the variation among individuals in response to the same level of food intake (Fig. 4). Often, different individuals made opposite responses: one spider building larger-than-average orbs and gaining little weight, another building smaller-than-average orbs and gaining weight rapidly. The variation was not a function of the sex nor of the initial size (TPL) of the individual (Fig. 4).

CONCLUSIONS

The two experiments uphold the predictions of the model. Juvenile *Nephila* of both species tended to increase orb-web size and decrease the rate of weight gain with slightly reduced prey capture; they decreased both orb-web size and rate of weight gain in response to greater reductions in prey capture. This response resulted in the counter-intuitive pattern of decreased foraging investment with low food availability, upholding the initial assumptions that resource allocation is constrained by a need to avoid weight loss and that common resources are used in foraging and growth in these spiders. At very low food levels, webs were small and few spiders gained weight but none lost weight. This food level is within the range captured in Panama, but much lower than median prey capture rates observed in Madang (4 prey/12 h diurnal observation) (Higgins & Buskirk 1992; Higgins, pers. obs.).

Nephila maculata juveniles varied greatly in their response to the experimental treatment. Such differences were not found in the experiment with *N. clavipes*, when the spiders were reared under homogeneous conditions. This difference might represent some intrinsic difference between species, but probably reflects differences in experience prior to the experiment. *N. maculata* juveniles were collected in the field, and undoubtedly differed in their foraging histories. The foraging history of an individual may cause it to respond in a particular fashion to changes in prey capture rates. This implies differences in the response to short *vs.* long term variation in prey capture, which cannot be examined by the short-term experiments presented here.

There is evidence that many spiders evolved under conditions of food limitation (Anderson 1974; Wise 1975, 1979). In web-building spiders, the web must be built before the foraging quality of a site can be assessed. Perhaps due to this initial investment, or due to temporal variation in prey availability, many web-building spiders are highly site-tenacious (Eberhard 1971; Enders 1976; Tanaka 1989; however, see Turnbull 1964). Rather than abandoning poor patches, a strategy often predicted by foraging theory (e. g., Charnov 1971; Pyke et al. 1977), spiders show other behavioral and physiological responses to nutritional stress (Riechert & Luczak 1982; Sherman 1994). However, these responses can slow growth and affect both survival and female fecundity (Higgins 1992a, 1992b, pers. obs.). The results of these studies support the hypothesis that there are potentially limiting resources necessary for both orb silk synthesis and growth, predicted by the chemical analyses of orb-silk by Tillinghast and Townley (Tillinghast 1984; Townley et al. 1991). The spiders must invest in the orb web in order to capture prey, but unless critical resources are in abundance, such investment necessarily delays growth and development and potentially compromises individual fitness. Predation rate declines with increasing spider size and fecundity increases with early maturation (Higgins 1992b, pers. obs.), so lengthening time between molts can have a detrimental effect on fitness. To avoid reduction in weight during periods of low food availability, the interactions between foraging investment and growth may be more complex than predicted by classical optimal foraging models.

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RESEARCH NOTES

NESTS OF *HIBANA GRACILIS* ARE REUSED BY *PHIDIPPUS CLARUS* IN WETLANDS OF NORTHEASTERN KANSAS

Typical nests of wandering spiders consist of small, tightly packed hollow bundles. In these nests spiders molt, retire for part of the day and often lay their eggs (Jackson 1979; Foelix 1982). Nests may be constructed on the ground in natural shelters such as leaf litter or woody debris or within a plant canopy among easily folded leaves or other structures (Johnson 1992).

In wetlands of northeastern Kansas in early May of 1993 and 1994, I found many mating pairs of *Hibana gracilis* (Hentz) (Araneae, Anyphaenidae) within nests made in the small up-

Figure 1.—Mating pair of *Hibana gracilis* (Araneae: Anyphaenidae) in the uppermost expanded leaves of the milkweed plant.

permost expanded leaves of common milkweed (*Asclepias syriaca*) and sullivant's milkweed (*A. sullivantii*) (Fig. 1). Because these milkweed species may be more common in annually burned wetlands (Johnson & Knapp, in press), I quantified the density and diversity of *H. gracilis* nests in three annually burned wetlands. Each wetland was approximately 350–500 m² in area and contained approximately 5.4 *A. syriaca* or *A. sullivantii* stems/m² (Johnson, in press). *Hibana gracilis* nests were found on 72% of milkweed stems in 40 plots, making nest density among milkweed in these wetlands 3.88 nests/m². Nests were observed in this density on either *A. syriaca* or *A. sullivantii* depending on which species was more centrally located within wetlands. Otherwise, *H. gracilis* nests were found within basal leaf sheaths of prairie cordgrass (*Spartina pectinata*) in a density of 0.4 nests/m² ($n = 30$ m² plots of *S. pectinata*).

By late May, *H. gracilis* had abandoned most nests; but the majority of these nests were reoccupied by *Phidippus clarus* Keyserling (Araneae, Salticidae). In the same three wetlands described above, 64% ($n = 40$) of former *H. gracilis* nests in milkweed stems were occupied by a female or a pair of *P. clarus*. Furthermore, these nests did not appear to have been altered in any way from the original structures made by *H. gracilis*. By mid-June 1994, *P. clarus* had also abandoned these milkweed leaf nesting sites.

This pattern of nest reuse represents an interesting interaction between wandering arachnids and may be linked to 1) shortage of suitable nesting sites, 2) reoccupation of optimal nest sites, or 3) silk conservation. Young milkweed plants may represent ideal nesting sites which are shared by sympatric arachnids with similar hunting methods and prey choices, but allochronic mating periods.

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Stephen R. Johnson: Division of Biology, Ackert Hall, Kansas State University, Manhattan, Kansas 66506 USA.

FLEXIBILITY IN FORAGING TACTICS OF *BUTHUS OCCITANUS* SCORPIONS AS A RESPONSE TO ABOVE-GROUND ACTIVITY OF TERMITES

Foraging modes are known to be generally fixed within a species, and flexibility of foraging tactics is often restricted by physiological and morphological traits, or by predation pressure (Huey & Pianka 1981). However, models and empirical evidence suggest that individuals may change foraging tactics as a response to variations in prey abundance (Schoener 1971; Stephens & Krebs 1986; Formanowicz & Bradley 1987). During research in the Negev desert of southern Israel in summer 1993, I observed scorpions of the species *Buthus occitanus israelis* switching foraging tactics as a response to sporadic above-ground activity of termites.

Buthus occitanus israelis is a burrowing scorpion found in arid zones of Israel and Sinai (adult body length 5–7 cm) (Levy & Amitai 1980). Like many other species of scorpions (Polis 1990), these are nocturnal, sit-and-wait predators that stand in ambush position some distance away from their burrows and locate prey by sensing air and soil vibrations. However, active foraging was observed as well and may constitute an alternative foraging tactic. Of all the individuals that were observed foraging on 30 nights (120 hours of observation), only 20% of the males and 12.5% of the females were moving, while most were motionless in ambush positions. When approached, these cryptic scorpions usually remained motionless, attempting to escape only if they were within 10 cm of their burrows.

Buthus occitanus scorpions are opportunistic, generalist foragers. Foraging scorpions in the field and in the laboratory accept various types of prey -- including crickets, Neuroptera, moths, bugs and various arachnids. However, in field observations, 70% of the scorpions consuming prey that could still be identified ($n = 27$), ate the wingless worker and soldier castes of harvester termites, *Anacanthotermes* sp. (specimens have been deposited at the National Collection in Tel-Aviv University).

These termites live underground and forage on the surface only in the vicinity of their burrows (usually within 70 cm of the entrance). When they encounter a predator they retreat into their nest within seconds. Observations revealed that widely-foraging *B. occitanus* scorpions approach the active termites and swiftly sting as many as possible before the termites disappear into the shelter of their burrow. The scorpion then moves around the area and collects the dead and dying termites with its pedipalps and chelicera. This foraging tactic was used by scorpions of all ages. On three occasions young scorpions were seen catching 1–2 termites at once, while on three other occasions large adult scorpions succeeded in collecting up to eight termites in a single attack.

In this unique foraging tactic *B. occitanus* scorpions exhibit a number of specialized behaviors that enhance the profitability of hunting for termites: a) since the termites forage within a small range around their burrow, the scorpion must actively forage for them rather than employ the usual sit-and-wait tactic; and b) termites are small and possess an effective alarm system. To use the short time available before the termites disappear, the scorpion must skillfully sting as many individuals as possible, without wasting time on handling and collecting. A comparable termite hunting tactic was observed in the web-building spider *Chrosiothes tonala* that specializes on termites (Eberhard 1991).

Collecting dead, motionless termites requires use of sense organs other than the mechanical receptors that are used by most scorpions to detect movement of live prey. Krapf (1986) showed in laboratory conditions that *B. occitanus* scorpions used contact chemoreception to detect motionless prey. Chemoreceptors may play an important role in hunting of termites, by allowing the scorpions to separate the short time available for attacking and subduing the prey from the time-consuming process of collecting and handling the dead prey.

Sit-and-wait foraging has been described as a low-cost, low-profitability strategy that may have evolved in species under predation pressure (Huey & Pianka 1981). By switching from their normal mode of ambush foraging into a widely-foraging mode of termite hunting, *B. occitanus*

scorpions may enjoy increased foraging success. However, a widely-foraging scorpion might also have to endure greater metabolic costs of foraging and increased risk of predation.

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BOOK REVIEW

Wise, D. H. 1993. Spiders in Ecological Webs. Cambridge University Press. ISBN 0-521-32547-1 (Price $79.95)

In this 328 page book, David Wise offers a comprehensive discussion of the literature on the use of spiders to test ecological models and theories. Until now, most books on spiders have been edited volumes that bring together the ideas of many others (e. g., Nentwig 1987; Shear 1986; Witt & Rovner 1982); equally valuable are the more general discussion of spiders (Foelix 1982) and taxonomic catalogs (Platnick 1989, 1993). David Wise's book is a welcome addition to this growing literature because he brings the focus of a single author while summarizing and providing a critique of the work of many researchers. His emphasis is on describing and critiquing field experimentation (especially in the context of studying competition), and on studying spiders both as predators and as models of generalist predators in terrestrial systems. He takes a look at spiders in agricultural systems as well. Wise brings his considerable experience as a community spider ecologist to his discussion and review of this literature.

There are nine chapters in this book, starting with one entitled "The Spider in the Ecological Play", which sets spiders as terrestrial, generalist predators onto the center stage of the ecological and evolutionary drama. This is followed by a progression of chapters first on hungry spiders (the importance of food limitation) and then series of chapters on competition: competitionist views of spider communities, failure of the competitionist paradigm and how (some) spiders may avoid competition. Following this explicit look at competition, there are chapters on the impact of spiders on insect populations, "anchoring the ecological web" (subtitled "refining the metaphor–the web's non-trophic threads" which is a look particularly at the architecture of the vegetation and leaf litter and how these factors affect the abundance of spiders), "untangling a tangled web" (in which Wise addresses "indirect factors" that help to structure complex communities, including intraguild predation), and finally, one entitled "spinning a stronger story" where Wise closely scrutinizes his own biases in the book.

Wise recognizes the limitation of the metaphor of spinning and webs that he uses throughout the book even as he attempts to use the metaphor to tease apart the threads of community structure. Each chapter begins with a 1–2 page introduction and concludes with a synopsis of the main ideas. The format makes the information in the book easily accessible. And while the book "hangs together" nicely as a whole unit, it is also easy to focus on one chapter at a time. I was able easily to go back to different chapters and find specific information.

The reference section includes 462 works. The literature spans from 1815 to 1992 with the bulk of the citations (249 entries) from the 1980's. Also included is a name index (for authors) and a subject index (with spider names and topics interspersed). The indexes are useful: the subject index includes family names, genus-species names and common names for the spiders. The name index works for second and third authors as well as for first authors.

Spiders in Ecological Webs will be of interest to a wide variety of ecologists, arachnologists and other biologists. I will use examples from this book in my 200-level Ecology class and will buy it for my school's (undergraduate) library. It will be useful to all researchers interested in spiders and/or interested in field experimentation. Wise's critiques of methods and statistics will be helpful to graduate students, professional ecologists and anyone planning field experimentation. For a variety of reasons, many researchers (including Wise, in his earlier days) have fallen into the trap of "pseudoreplication" in planning and carrying out field studies – Wise provides a particularly useful and extensive discussion of this problem. Because of this critique, *Spiders in Ecological Webs* will be useful in Biostatistics courses or in Research Methodology courses as well.

This book has several strengths. Clearly one of these is the detailed attention to studies of spiders in competition and studies of competition in which spiders play a big role. Wise clearly

shows through this discussion how ideas about competition have changed dramatically in the last few decades. He very capably discusses the question "Is there evidence that spiders compete or that competition is important in structuring ecological communities?" A second major strength of the book is Wise's attention to field studies and field manipulation and experimentation. This emphasis makes this work useful to a wide range of ecologists, even those without an interest in arachnids. However, the central strength of the book lies in Wise's willingness to present a wide variety of studies, critique them closely, reanalyze data if need be and show how (even with a particular study's weakness), insights can be gleaned from it. For example, the study by Clarke & Grant (1968) (discussed on pp. 147ff) is a classic study in leaf litter ecology and probably introduced the idea of field manipulation to many ecologists. This study has been cited to support the idea that spiders have a significant impact on insect populations in leaf litter ecosystems. While this is an important and classic paper, Wise explains its flaws in terms of experimental design (in this case, primarily a lack of replication). This study has been followed by a variety of manipulative field experiments by Bultman & Uetz, Wise & Wagner and Kajak & Jakubczyk, among others. I think some of the manipulations done by later researchers would have amazed Clarke and Grant.

Throughout reading the book, I felt a sense that there really is progress in science. You can see through the reviewed literature that studies *have* been done more and more carefully and researchers *have* learned what is necessary to tackle a problem appropriately and in many cases have designed and executed experiments that ecologists didn't even imagine 20 years ago as in the case with Clarke and Grant.

To his credit, Wise does not hesitate to criticize his own research. In Chapter 5, "How spiders avoid competition," he reworks much of his own data and in some cases, comes to different conclusions. For example, following his reanalysis, he finds that contrary to his earlier assertions, there is no evidence that intraspecific competition affects fecundity in spring maturing filmy dome spiders. To me, this is the epitome of science – when an individual synthesizes from his/her own work and from the work of others and moves forward in understanding a particular system.

Wise does not cover the extensive and growing literature on spider behavioral ecology, nor does he attempt to cover the realms of spider evolutionary ecology or sensory ecology. Tackling these broad topics would have completely changed the nature of the book and probably would have made it prohibitively large. Other books on these topics remain to be written.

Although there is some discussion of cursorial spiders, Wise emphasizes web building spiders in the northern hemisphere probably because many ecological studies have been on web builders in the northern hemisphere. Something Wise does *not* do in this book is to remind the readers of the number of terrestrial ecosystems that have not been studied as extensively by field experimentalists. I wonder what a "model spider" would be in a tropical system where the vast majority of collected spiders are "singletons"? Such systems are much more difficult to manipulate, yet because of the vastness of the tropical biome, generalities without considering it are problematic. I think it is always useful to put our knowledge in context – to remind ourselves of the bigger picture and what and how much we do *not* know. It is also worth mentioning that we probably still know only a fraction of the all of the spider species. What is a "general spider" (a term Wise uses), and can we know if, as Coddington & Levi (1991) suggest, only 20% of the world's spider fauna is known? There are more species of Salticidae than any other family, and among the six most speciose families, there are more species of non-web builders (8800 species) than there are of web building spiders (8500 species) (Coddington & Levi 1991). Perhaps a "general spider" should be a salticid spider from a tropical biome.

Some of Wise's terminology is problematic. For example, his use of the group "cribellate spiders" (p. 6) is unfortunate as this no longer a valid grouping (Coddington 1990). Also unfortunate is Wise's groupings of "closely related species" –such as the Agelenidae and the Lycosidae (p. 8) – two families that are not particularly close (Coddington & Levy 1991). Wise only briefly touches on the very interesting phenomenon of sociality in spiders, particularly in tropical areas. Perhaps that will be covered in a another book on evolutionary ecology in spiders.

While I was bothered at first by Wise's attempt to generalize a single "spider persona", I found myself enjoying the book more and more as I read through it. I particularly enjoyed being able to trace a series of papers done by one person

(or group of persons) and be able to see the evolution of thinking in various spider ecologists. It was also very helpful to see how frequently many researchers have tackled a particular problem; and taken together, we really do have a lot of insight on particular questions. I got a sense of continuity from this and satisfaction that I could go to one source and find such useful summaries and find so many references.

On the whole this is a welcome addition to both the spider literature and the ecological literature. I think Wise's goal of introducing spiders to a wider ecological audience will be met in this book. It will also make accessible a large ecological literature to other arachnologists. The book left me hopeful on several counts – I hope that the momentum of research of the 1980's continues through the 1990's and into the next century. I hope future editions will take into account more from tropical ecosystems – and that there will be more research to report and summarize from other regions. And finally, I hope there will be other books on spider behavioral ecology and evolutionary ecology. It is an exciting time to be working on spiders.

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Gail E. Stratton. Dept. of Biology, Albion College, Albion, Michigan 49224 USA

BOOK REVIEW

Platnick, N. I. 1993. *Advances in Spider Taxonomy 1988-1991 With Synonymies and Transfers 1940-1980* (edited by P. Merrett). The New York Entomological Society, New York.

Ask any reasonably competent biologist and you will be told that evolution is change or advance but that change does not necessarily equal progress. Advances may be made to the rear. Science has evolved (advanced) by leaps and bounds sideways, backwards, tangentially, and occasionally (but generally, I believe) forward over time. This evolution has been guided in part by the blinders of religious and political ideologies and the vagaries and frustrations of funding, peer review, turf wars, hidden agendas, and a bewildering array of "refereed" publications. Thus have spider taxonomy and systematics evolved over the last two centuries: a generally progressive trend emerging from apparent chaos as myriads of independent workers have pursued their independent taxonomic agendas under the one common (but vague) guiding principle of discovering (real or imagined) order in the confusing profusion of life forms. Battles rage, die, and then flare up again over species concepts and systematic methodologies but some constants remain. First a species is whatever a researcher can convince his or her colleagues it is. Second, and more important, at the roots of all good biology are good phylogenies. Third, and most important, good phylogenies are rooted in good taxonomy. The end result of all this is names and publications. Many, many names in many, many publications. That advances (progress) have been made at all in spider taxonomy and systematics is, at least in part, due to the unique and increasingly useful and user-friendly series of spider taxonomic catalogues culminating in the most recent volume by Norman Platnick.

Others have discussed the merits and shortcomings of the araneological catalogues of Bonnet, Roewer, and Brignoli. In spite of the serious problems caused by Brignoli's omission of synonymies and transfers of pre-Roewer names these works have been of immense value. Platnick's two volumes have continued and improved upon the works of his predecessors. The first, *Advances in Spider Taxonomy 1981-1987* (1989), kept abreast of post-Brignoli developments listing citations of illustrated taxonomic works and cataloguing new names, synonymies, and transfers published from 1981 to 1987. The second (current) volume does the same for the period 1988 to 1991 with the added bonus of listing all the synonymies and transfers omitted by Brignoli (1940–1980). It is now possible, as Platnick (with some modesty) points out in his introduction, ". . . using Roewer and the three supplemental volumes [of Brignoli and Platnick], to determine what genera belong to each family (along with their synonyms) and what species belong to each genus (along with their synonyms)". This has been no mean feat but the catch-up job remains incomplete in one area. Still lacking are the citations for the post-1940 literature containing illustrated redescriptions not involving transfers or synonymies. It is hoped that this data (*circa* 1.5 megabytes) will be presented in the next supplement (Platnick, pers. comm.), pending adequate funding. *Stet fortuna domus.*

The current catalogue is a weighty tome (846 pages) and much less visually exciting than the most recent catalogue from L. L. Bean. However, unlike the latter, the usefulness of *Advances in Spider Taxonomy 1988–1991* is not time constrained and I noted no apparent errors within it, typological or otherwise. A short tribute to the long standing, competent, and quiet technical support of Louis Sorkin is an appropriate opening to the volume. Following this, the Introduction outlines Platnick's rationale for deciding what to include in, what to omit from, and the presentation format of his treatment. Platnick notes that the material presented is split roughly in half between new literature published from 1988 through 1991 and the synonymies and transfers missed in the previous catalogues. An effort has been made to avoid repetition of material sufficiently treated in the previous works. This has kept the published bulk to a manageable size but also means that researchers still need a complete set of Roewer (and/or Bonnet), Brignoli, Platnick, and Platnick to have as thorough a treatment of the taxonomic picture as is probably possible. Formatting of *1988–1991* follows the style of *1981–1987*.

A list of families shows we are *status quo* with respect to the number (105) listed in *1981–1987*. A comparison of the two lists reveals minor changes including three new families (Synotaxidae, Trechaleidae, Lamponidae) and two resurrections (Zoropsidae, Prodidomidae) balanced by five sinkings (Loxoscelidae, Hadrotarsidae, Dolomedidae, Platoridae, and Aphantochilidae absorbed by Sicariidae, Theridiidae, Pisauridae, Trochanteriidae, and Thomisidae, respectively). Families are listed in a one-dimensional reflection of the current consensus of opinion on classification. The family lists of Brignoli and *1981–1987* reflected the major upheavals in spider classification resulting from the 1967 trashing of Cribellatae by Lehtinen and the general acceptance through the 70's and 80's of cladistic methodology as the best way to divorce art from science in classification. It is somewhat of a relief to see no evidence in *1988–1991* of new major changes. Advance (progress) in spider higher classification during this short period has been limited to the support by Platnick et al. of the monophyly of Haplogynae (16 families from Filistatidae to Orsolobidae). This leaves only the question of the monophyly of the major (and troublesome) "RTA clade" (43 families from Lycosidae to Salticidae) unanswered (in spite of some excellent work within this group by Griswold, Platnick, Sierwald, and others on "dictynoids", gnaphosoids, "amaurobioids", and lycosoids). Life continues.

The Bibliography lists by year approximately 1700 publications referenced in the text. A small handful (38) covers works from 1867 to 1939 missed or with material excluded from the previous catalogues (or otherwise needing repetition). Over 900 entries relate to the synonymies and transfers from 1940 to 1980 omitted by Brignoli. Some 73 references from 1981 to 1987 cover mostly material missed by *1981–1987*. The remaining 653 references (averaging a fairly consistent 160 per year) are the new taxonomic publications appearing around the world from 1988 to 1991. From there we go into the meat of the matter.

Sanity constraints dictated that I concentrate my review efforts upon a particular aspect of the approximately 750 pages of the Catalog of Genera and Species. Synonymies of genus names and transfers and synonymies of species names are adequately cross-referenced under the appropriate family and genus headings. Every currently valid genus name is presented. All this is immediately evident from a casual inspection of the listings and is also explained in the Introduction. In my review of this section I did not make an attempt to keep track of the new sinkings and other changes but concentrated on tallying up new species and genus names appearing from 1988 to 1991. This process was logistically simple, was an adequate indication of in what groups research is most active, and gave me an idea of how close we have come to the mythical figure of 40,000 described spider species.

Roughly 180 new genera and 2070 new species were described during the four year period 1988–1991. In comparison to Coddington's counts of 230 and 2581 for new genera and species described in the preceding seven year period there appears to be some consistency in a new species to new genera ratio of about 11:1 coupled with a substantial upswing in the curve of descriptive activity. Obviously there are still lots of spider species out there to be described and the reduced cadre of professional taxonomists is working harder than ever on the task. Further comparison of these figures with Platnick's earlier estimate of roughly 3000 and 34,000 described genera and species in total shows the 11:1 ratio also is consistent with the historical trend in spider taxonomy. Without considering new synonyms about 36,000 spider species have now been described. Coddington and Levi recently presented statistics in support of an estimate of approximately 170,000 extant spider species. In a world reluctantly coming to acknowledge a) the cardinal importance of arthropods in the faunal component of all ecosystems and b) the historical "megafaunal" bias in zoological inquiry (discussed by Platnick elsewhere), perhaps there is cause for renewed hope for the future of spider taxonomy. What could we do with some serious funding for baseline "biodiversity" inventories?

All the following species and genus numbers above 50 are approximate and rounded to the nearest 10. Not surprisingly, new genera and species in the suborder Opisthothelae (104 families, 180 new genera, 2060 new species) vastly outnumber those in Mesothelae (1 family, no new genera, 14 new species). Similarly the bulk of new descriptions in Opisthothelae are in Araneomorphae (89 families, 180 new genera, 1960 new species). Mygalomorphae (15 families) has 5 new genera and 90 new species. Further down the araneomorph classificatory trail it is hardly surprising there has been no activity among the paleocribellates (I mean, how many new hypochil-

ids do you expect there are left to find?) or the austrochiloid neocribellates (ditto).

Within Araneomorphae (and Araneae in general) Araneoclada is where the action is hottest and some observations of descriptive trends within this grouping (note that four genera account for well over 10% of all new spider species described) have prompted my proposal for a series of awards suggested below. The newly verified group Haplogynae (16 families) shows five new genera and 120 new species (nearly 90 of which are in the two dysderid mega-genera *Dysdera* and *Harpactea*). Entelegynes, of course, account for all the rest. Most activity was registered in Araneoidea (11 families) with nearly 130 new genera and 1060 new species. Paramount in this superfamily are the linyphiids with over 80 new genera (many of which are monotypic) and nearly 560 new species. This accounts for close to half of all new genera and over one quarter of all new species in the entire order Araneae. Other notables within Araneoidea include the synotaxids (10 new genera, 50 new species), theridiids (3 and 52), anapids (21 and 60) and araneids (6 and 300). Fully two-thirds of the araneid new species are in the two mega-genera *Araneus* and *Alpaida*. One can only hope that with this level of activity we must be getting close to resolving the familial relationships within Araneoclada.

The "RTA clade" has been relatively quiet (44 new genera, 740 new species) given its size (43 families). Salticid descriptions account for about a quarter of the new names with 11 new genera and 180 new species. Zodariids have 14 new genera and nearly 90 new species; amaurobiids have 7 and 110 (with over 60 new species in *Coelotes*). Clubionids and gnaphosids each have one new genus and over 50 new species (49 in *Clubiona*); thomisids have over 50 new species as well. "Also ran" RTA's include the lycosids (1 new genus, 39 new species) and heteropodids (3 new genera, 30 new species).

For some years the araneological world has been poised, somewhat breathlessly, awaiting new revelations into the nature of the RTA clade (is it real or just an infatuation?) and its putative major sub-groupings Dionycha (22 families) and the "dictynoids" (7? families), "amaurobioids" (4? families), and lycosoids (10? families). Dictynoids and amaurobioids, with their tattered and torn remnants of many of the old, pre-Lehtinen cribellate groupings, pose the biggest problems for systematists (just what is a cybaeid, a dictynid, a hahniid, an agelenid, or even an amaurobiid anyway?) and yet *1987–1991* shows very little work (with the exception of Amaurobiidae) in these groups. The calm before the storm. . .?

Concluding the Catalog is a short listing of all new nomenclatorial changes to be found in the previous 750 pages. Surprisingly there are very few and wherever possible Platnick has used new names provided by the original authors. Thus there are nine and 11 new synonyms, replacement names, or transfers of genera and species respectively. All the specific synonymies are from Platnick's own work with gnaphosid type material.

At this point, with tongue firmly planted in cheek (and hoping none take offense), I would like to propose the creation of the R. V. Chamberlin Araneological Olympics with awards presented to recognize conspicuous advances in araneological taxonomy. For the first such Olympics I have identified a small number of competitive categories and chosen award winners from the listings in 1988–1991. Certainly someone with a more active imagination and better database skills than I could expand upon the following. For "Most Species Described in One Genus" the gold medal goes to the United States for H. W. Levi's work with *Alpaida* (94 new species), the silver goes to England (A. F. Millidge, 79 new species in *Dubiaranea*), and the bronze to the United States (H. W. Levi again, 71 new species in *Araneus*). For "Most Monotypic New Genera in One Family" the gold medal is awarded to England for A. F. Millidge's 25 new genera in Linyphiidae (no silver or bronze medals were awarded in this category). For "Most Species Transferred to Other Genera" the clear winner of the gold medal is *Araneus* (363 transfers). In a distant second place the silver medal winner is *Dendryphantes* (210 transfers). Finally, there is one award to be presented in the N. I. Platnick Araneological Special Olympics for "Best New Name." This category has been inspired generally by the evidence of subtle taxonomic humorists among our ranks and specifically by the spooneristic, cinematically inspired name *Apopyllus now* ("an arbitrary combination of letters" indeed). Undoubtedly the following presentation is debatable, based as it is upon the decision of one judge, but for the period 1988 to 1991 the winner is Poland for W. Zabka's new genus and species *Abracadabrella birdsville*. Congratulations to all.

In closing I do not apologize for quoting from

Coddington's review of the previous volume. ". . . *Advances in Spider Taxonomy [1988–1991]* is a splendid volume. I do not have to recommend that you buy it, because you already know that it is indispensable. Arachnologists and beyond owe Platnick a fervent thanks, because few works are as critical to good biology as nomenclatorial catalogs. If taxonomy is the *sina qua non* of all biological science, it is because of works such as this." Here is an advance that definitely equates with progress.

Robert Bennett: British Columbia Ministry of Forests,7380 Puckle Road, Saanichton, British Columbia V8M 1W4 Canada

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(revised July 1995)

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Figures 1–4.—*A-us x-us,* male from Timbuktu: 1, left leg; 2, right chelicera; 3, dorsal aspect of genitalia; 4, ventral aspect of abdomen.
Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33, dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28, *A-us x-us,* holotype male; 33, 34, *A-us y-us,* male. Scale = 1.0 mm.

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Cover illustration: Scanning electron microscope photograph of the abdomen of a mature female *Philoponella vicina* (Uloboridae). Photograph by Flory Pereira and William G. Eberhard.

DESCRIPTION OF THE SPIDER
MASONCUS POGONOPHILUS (ARANEAE, LINYPHIIDAE),
A HARVESTER ANT MYRMECOPHILE

Paula E. Cushing: Department of Zoology, University of Florida, Gainesville, Florida 32611 USA

ABSTRACT. One species of the genus *Masoncus* (Araneae, Linyphiidae) is described and illustrated. *Masoncus pogonophilus* new species has been collected exclusively inside the nests of the Florida harvester ant, *Pogonomyrmex badius* (Latreille) (Hymenoptera, Formicidae) and is, therefore, considered a myrmecophile, or obligate ant associate. Morphological characters separating this new species from two of the three described congeners (*M. arienus* and *M. conspectus*) are noted.

Three species are included in the genus *Masoncus* Chamberlin 1948: *M. arienus* Chamberlin 1948, *M. dux* Chamberlin 1948, and *M. conspectus* (Gertsch & Davis 1936) (synonymized with *M. nogales* Chamberlin 1948 by Ivie 1967). The female holotype of *M. dux* has been lost and I was unable to locate any specimens of this species. The female holotype, male allotype and paratypes of *M. nogales* designated by Chamberlin (1948) have also been lost. However, the holotype of *Tapinocyba conspecta* is housed at the American Museum of Natural History in New York City, New York (AMNH) as are other representatives of this species. The holotype and paratypes of *M. arienus* designated by Chamberlin (1948) are also at AMNH. One male representative of *M. arienus* is housed at the California Academy of Sciences in San Francisco, California (CAS).

No information was recorded either in the original species descriptions or on the collecting labels of the existing specimens regarding the natural history of the described species. *M. dux* was described from a single female collected in northern Manitoba, Canada. All specimens of *M. arienus* were collected in Arizona. *M. conspectus* was described from the male holotype and two male paratypes collected in Texas. Other records of this species include Arizona and Florida (the latter collected by the shores of Newnan's Lake in Alachua County).

Masoncus pogonophilus new species was originally collected by Sanford Porter from the nests of the Florida harvester ant, *Pogonomyrmex badius* (Latreille) (Hymenoptera, Formicidae) (Porter 1985). It is included in the genus *Masoncus* due to the presence of distinct cephalic

pits and a straight, distally bifid embolic division in the males (see genus description below).

In the species description that follows, I use primarily carapace, genitalic, chaetotaxic, numeric, and palpal characters deemed most useful by Millidge (1980) for erigonine spiders. These characters include: 1) the overall conformation of the male palpal organ, 2) the shape of the embolic division, 3) the external appearance of the epigynum, 4) the number of dorsal trichobothria present on the palpal tibia of both sexes, 5) the number of dorsal tibial spines present (expressed by the formula a:b:c:d), 6) the number of dorsal metatarsal trichobothria present (expressed by the formula I:II:III:IV), 7) the relative position of the dorsal metatarsal trichobothrium on leg I (expressed by the formula TmI = distance from tibia-metatarsus joint to trichobothrium/distance from tibia-metatarsus joint to metatarsus-tarsus joint), and 8) the relative stoutness of tibia I (expressed by the formula TibI = length of tibia/width of tibia viewed laterally). Overall body size, body color, and number of setae on the carapace are also given. Certain of these characters as well as others used in Chamberlin's (1948) descriptions or obvious on the existing specimens are of particular value in separating *M. arienus*, *M. conspectus*, and *M. pogonophilus* (Table 1). All measurements were taken directly from the specimens using an ocular micrometer in a dissecting microscope. Measurements were rounded to the nearest 0.1 mm.

Masoncus Chamberlin 1948

The type species of the genus is *M. arienus*. The genus *Masoncus* is characterized by both cephalic pits in the males and a straight, distally

Table 1.—Morphological characters most useful in separating three of four *Masoncus* species. (All specimens of *M. dux* are lost, and the species description is based solely on the female holotype.) pme = posterior median eyes.

Characters	*M. arienus*	*M. conspectus*	*M. pogonophilus*
Location of cephalic pits in males	Pit opens back of posterior eyes; not extending under pme	Pit opens and extends beneath pme	Pit opens and extends beneath pme
Cheliceral spurs towards distal end	Present on males and females	Present on males; reduced to very small black spurs on females	No cheliceral spurs on males or females
Setigerous nodule or spur anterior to fang groove	Nodule present on males and females	Spur on males; lacking on females	No setigerous nodule or spur on males or females
Endites with small spur on ectal side of tip	Present on males and females	Present on males and females although less distinct on latter	No spurs on endites of males or females
Shape of palpal tibia	Widely spaced black-tipped processes on distal edge flush w/ surface of tibia; long setal fringe on lateral edge	Closely spaced black-tipped processes on distal edge extending slightly away from surface of tibia; long setal fringe on lateral edge (fig. 97 in Chamberlin 1948)	Moderately spaced black-tipped processes on distal edge flush w/ surface of tibia; long setal fringe on lateral edge (see fig. 4)
Embolic division	Bifurcation begins close to tail-piece; each segment of bifurcation coiled (fig. 101 in Chamberlin 1948)	Distally bifid w/ proximal part of bifurcation bent forward and extending over most distal part which is, itself, squared off (fig. 98 in Chamberlin 1948 shows it pointed)	Distally bifid w/ proximal part of bifurcation bent forward and extending over most distal part which is, itself, bifurcated (see Fig. 3)

bifid embolic division (Chamberlin 1948) (diagram of linyphiid palpal structures in Millidge 1980).

Masoncus pogonophilus new species
(Figs. 1–5)

Type.—The male holotype was collected 23 cm below ground inside a nest chamber of the Florida harvester ant, *Pogonomyrmex badius* in Archer Sandhills, 1.4 km west of the Levy County line off of State Road 24. The female allotype was collected from the same *P. badius* nest. She was found in a nest chamber 46.5 cm below ground. Both were collected on 25 September 1994 and both will be deposited in the arachnological collection at CAS.

The holotype, 11 male paratypes, the allotype, and 12 female paratypes were used in this species description. The collecting information as well as the future museum destination for these paratypes are presented in Table 2.

Etymology.—The specific epithet is derived from the generic name of the host ant with which the spider is found.

Holotype.—Total body length: 1.7 mm. Carapace length: 0.9 mm. Carapace width: 0.7 mm. Colors: carapace orange; abdomen grey; legs orange; sternum orange. Number of setae along midline of carapace: three. Palp as in Fig. 3. Embolic division as in Fig. 4. Number of trichobothria on palpal tibia: two (Fig. 2). Number of dorsal tibial spines: 1:1:1:1. Number of dorsal metatarsal trichobothria: 1:1:1:0. TmI: 0.82. TibI: 7.0.

Males (general).—($n = 12$). Total body length: 1.6–2.1 mm ($\bar{x} = 1.8 \pm 0.14$). Carapace length: 0.8–0.9 mm ($\bar{x} = 0.9 \pm 0.04$). Carapace width:
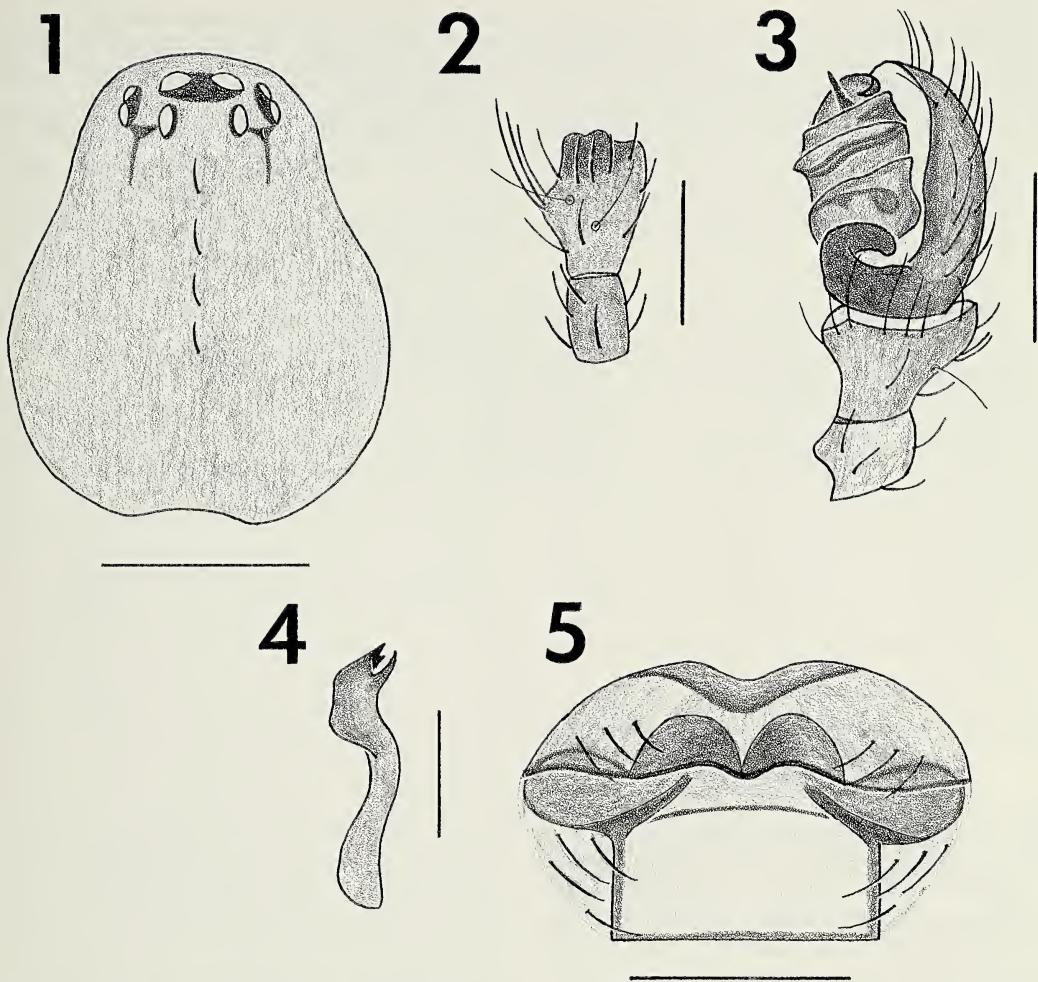
Figures 1–5.—*Masoncus pogonophilus* new species. 1, male carapace, dorsal view (scale = 0.4 mm); 2, tibia and patella of left male palpus, dorsal view, trichobothria in circular pits (scale = 0.2 mm); 3, male palpus, prolateral view (bifurcation of embolic division just visible distally) (scale = 0.2 mm); 4, embolic division of left male palpus, mesoventral view (scale = 0.1 mm); 5, epigynum, ventral view (scale = 0.1 mm).

0.6–0.8 mm ($\bar{x}$ = 0.7 ± 0.05). Colors: carapace yellow-orange to orange; abdomen grey; legs yellow-orange to orange; sternum yellow-orange to orange. The color seems to fade severely when specimens are kept in isopropanol rather than ethanol. Number of setae along midline of carapace (Fig. 1): variable, 2–4 (setae easily broken in preservation). Palp as in Fig. 3. Embolic division as in Fig. 4. Number of trichobothria on palpal tibia: generally two (Fig. 2), however one male had two on the left palpal tibia and three on the right and another had three on the left and two on the right. Number of dorsal tibial spines: 1:1:1:1. Number of dorsal metatarsal tri-

chobothria: 1:1:1:0. TmI: 0.82–0.88 ($\bar{x}$ = 0.84 ± 0.02). TibI: 6.5–7.7 ($\bar{x}$ = 7.0 ± 0.35).

Females.—(n = 13). Total body length: 1.5–1.9 mm ($\bar{x}$ = 1.8 ± 0.13). Carapace length: 0.8–1.2 mm ($\bar{x}$ = 0.9 ± 0.11). Carapace width: 0.6–0.9 mm ($\bar{x}$ = 0.7 ± 0.09). Colors: same as males. Number of setae along midline of carapace: variable, 2–5; females also had smaller setae scattered on either side of midline. Epigynum as in Fig. 5. Number of trichobothria on palpal tibia: generally three, however one female had two on both palps, three other females had three trichobothria on the left palpal tibia and two on the right. Number of dorsal metatarsal trichoboth-

Table 2.—Collection information and museum destination for the 23 paratypes. All were collected from the nests of the Florida harvester ant, *P. badius*. MCZ = Museum of Comparative Zoology, Cambridge, Massachusetts; DPI = Division of Plant Industry, Gainesville, Florida; AMNH = American Museum of Natural History, New York, New York; CAS = California Academy of Sciences, San Francisco, California.

Collection date	Florida county	Collector	Number of specimens	Museum
Males				
10- XI-1982	Leon	S. D. Porter	1	MCZ
9- XI-1984	Leon	S. D. Porter	1	MCZ
13- I-1990	Walton	Skelley, Turnbow & Thomas	2	DPI
14- I-1990	Okaloosa	Skelley, Turnbow & Thomas	1	DPI
9- V-1992	Leon	P. E. Cushing	1	DPI
26- V-1992	Levy	P. E. Cushing	2	AMNH
8- X-1992	Levy	P. E. Cushing	1	AMNH
20- II-1993	Levy	P. E. Cushing	1	CAS
25- IX-1994	Levy	P. E. Cushing	1	CAS
Females				
3- I-1990	Okaloosa	P. Skelley	1	DPI
13- I-1990	Walton	Skelley, Turnbow & Thomas	1	DPI
9- V-1992	Leon	P. E. Cushing	1	DPI
28- II-1993	Putnam	P. E. Cushing	4	AMNH
25-VII-1993	Putnam	P. E. Cushing	1	MCZ
25- IX-1994	Levy	P. E. Cushing	4	CAS

ria: 1:1:1:0. TmI: 0.58–0.87 ($\bar{x}$ = 0.81 ± 0.09). TibI: 6.5–7.9 ($\bar{x}$ = 7.1 ± 0.38).

Diagnosis.—The carapace of male *M. pogonophilus* most resembles that of *M. conspectus* (fig. 93 in Chamberlin 1948 and Fig. 1). In both species, the cephalic pits extend beneath the posterior median eyes (pme) whereas in *M. arienus* the cephalic pits open behind the pme. The embolic division of male *M. pogonophilus* new species most resembles *M. conspectus* (fig. 98 in Chamberlin 1948 and Fig. 4) in that both are distally bifid with the proximal part of the bifurcation bent forward and extending over the most distal part of the bifurcation. However, in *M. pogonophilus* the most distal part of the bifurcation is, itself, bifurcated, whereas in *M. conspectus* it is flattened (although fig. 98 in Chamberlin 1948 shows it to be pointed). In *M. arienus* the embolic division is also bifid, but the bifurcation begins very close to the tailpiece and each segment of the bifurcation is coiled (see fig. 101 in Chamberlin 1948). The male palpal tibia of the new species, as with *M. conspectus* and *M. arienus,* is fringed laterally with long setae (Fig. 2). Chamberlin 1948 (fig. 102) does not show this fringe of setae on his drawing of *M. arienus* but it is evident on the preserved specimens. All three species have two black-tipped processes on the distal edge of the palpal tibia (Fig. 2). These processes are more widely spaced in *M. arienus* than in either *M. conspectus* or in *M. pogonophilus*. The black-tipped process in *M. conspectus* is found on a slight ridge that extends away from the surface of the tibia (fig. 97 in Chamberlin 1948). Interestingly, *M. conspectus* is the only one of the three previously described congeners whose known distribution extends into northern Florida. The new species can be sepa-

Figure 6.—Sticky silk from adult male *Masoncus pogonophilus* new species web. Magnification 400×.

rated from the congeners based primarily upon characters described in Table 1 as well as upon overall size; the new species being somewhat smaller than *M. dux*, *M. arienus* and *M. conspectus*, which are all between 2.10–2.65 mm in length according to Chamberlin (1948) and Gertsch & Davis (1936).

Natural History.—*Masoncus pogonophilus* new species lives within the nest chambers of the Florida harvester ant, *P. badius*. It is about ¼ the size of its 7–9 mm long host and feeds on collembolans found throughout the 1–3 m deep subterranean nests (Porter 1985). The ant nest provides a stable microclimate as well as an abundant food source for the spider. The spiders have never been collected outside the ant nests and are extremely susceptible to desiccation when removed from the nests. They appear, therefore, to be obligate ant symbionts, or myrmecophiles.

Immigration to new nest sites is common in *P. badius* (Gentry & Stiritz 1972; Golley & Gentry 1964; Gordon 1992). While observing three such colony migrations, each occurring either just after a summer shower or in the early morning when the surface temperature was cool and the humidity high, I saw spiders and collembolans moving from the old colony site to the new amidst their host ants within the emigration trails. Using a PCR (polymerase chain reaction)-based molecular technique, I have also found evidence that spiders disperse between neighboring ant nests (pers. obs.).

Both sexes of *M. pogonophilus* build prey capture webs in the lab, and I have seen webs inside the ant nest chambers. Both males and females produce sticky silk (Fig. 6). Therefore, males presumably retain the aggregate and flagelliform glands into adulthood; most adult male spiders lose these glands during the terminal molt and cannot subsequently produce sticky silk (Kovoor 1987). Maintaining the ability to produce sticky silk as adults may be common among male erigonine Linyphiids as I have observed such behaviors among other (unidentified) male erigonines.

Female *M. pogonophilus* lay 1–6 eggs in a disk-shaped eggsac deposited in a depression in the wall of a nest chamber ($n = 9$ eggsacs, $\bar{x} = 2.9 \pm 1.5$ eggs/eggsac). The eggsac is flush against the surface of the chamber walls. Juvenile spiders molt once inside the eggsac and pass through three additional molts before reaching maturity.

Juveniles are present inside the ant nests during all months of the year (Porter 1985; pers. obs.). Porter reported a 4:1 female-biased sex ratio among the spiders, while I have found an even more extreme 7.5:1 female-biased ratio. Due to the scarcity of eggsacs and the small number of eggs per eggsac, it has not been possible to determine whether this is a primary sex ratio bias.

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A TEST OF THE CENTRAL-MARGINAL MODEL USING SAND SCORPION POPULATIONS (*PARUROCTONUS MESAENSIS*, VAEJOVIDAE)

Tsunemi Yamashita[1] and **Gary A. Polis:** Department of Biology, Box 1812 Station B, Vanderbilt University, Nashville, Tennessee 37235 USA

ABSTRACT. The central-marginal model proposes marginal populations contain a lower density of individuals, lower levels of genetic variation, and are more isolated than populations in the center of a species range. Previous tests of the model used *Drosophila*, organisms capable of extended dispersal. We test the central-marginal model with scorpions, organisms with restricted dispersal abilities. We measured genetic variation through allozyme analysis of eight loci (five polymorphic, three monomorphic) to obtain estimates of heterozygosity. We compared differences between the two types of populations with a split-plot ANOVA. We also compared central and marginal populations using standard parametric tests. We found marginal populations contain lower genetic variation than central populations. These populations may be important as models in conservation to study the effects of fragmentation.

Peripheral or marginal populations are those on the boundaries of a species' geographic range. They exhibit unique properties not evident in populations in the center (Brussard 1984). Generally, as one moves outward from the center of a species' range, populations are hypothesized to become less dense, more isolated, and less variable genetically within populations (da Cunha et al. 1959; da Cunha & Dobzhansky 1954; Carson 1959; Soule 1973; Brussard 1984). These trends are embodied in the central-marginal model (Lewontin 1974). Several explanations exist. One hypothesis (da Cunha & Dobzhansky 1954) states genetic polymorphism is positively correlated with the number of niches an organism occupies — more niches are available at the center of a species range. Yet Brussard's (1984) free recombination hypothesis proposes linkage disequilibrium is favored in central populations because extreme phenotypes are selected against, i. e., stabilizing selection occurs. Here, favored genes are linked together to create a stable phenotype with maximal fitness. In theory, at the range margins, linkage equilibrium is selected in stressful environments to create novel phenotypes better able to survive sub-optimal conditions (Brussard 1984).

Research with *Drosophila* suggests the predic-

tion that allozyme heterozygosity is reduced at range margins is not valid (Brussard 1984). However, *Drosophila* probably disperse relatively great distances compared to most non-flying taxa. Non-flying taxa (vertebrates) show a decline in allelic diversity in marginal populations (Soule' 1973). We propose scorpions, unable to disperse great distances, also may illustrate the predictions of Lewontin's (1974) central-marginal model.

METHODS

Relevant scorpion biology.—The scorpion *Paruroctonus mesaensis* Stahnke is restricted to sand dunes and sandy substrates scattered throughout the southwestern United States and northern Mexico. It occurs in dense populations (range = 1600–5000/ha) (Polis & Yamashita 1991) and it is an ecologically important species, as a generalist predator in desert food webs (Polis 1979; Polis & McCormick 1986, 1987). This scorpion is dispersal limited because specialized morphological features adapt and restrict it to sand. The species possess numerous modified setae on their tarsi (sand shoes) to facilitate sand movement and burrow construction (Polis et al. 1986). Further, their ability to detect substrate vibrations to localize prey only functions well on sand (Brownell & Farley 1979). These specializations reduce the likelihood of extended migration. However, reproductive males move extensively when searching for mates (Polis & Farley 1979, 1980).

[1]Present address: Department of Biology, Northeast Louisiana University, Monroe, Louisiana 71209 USA
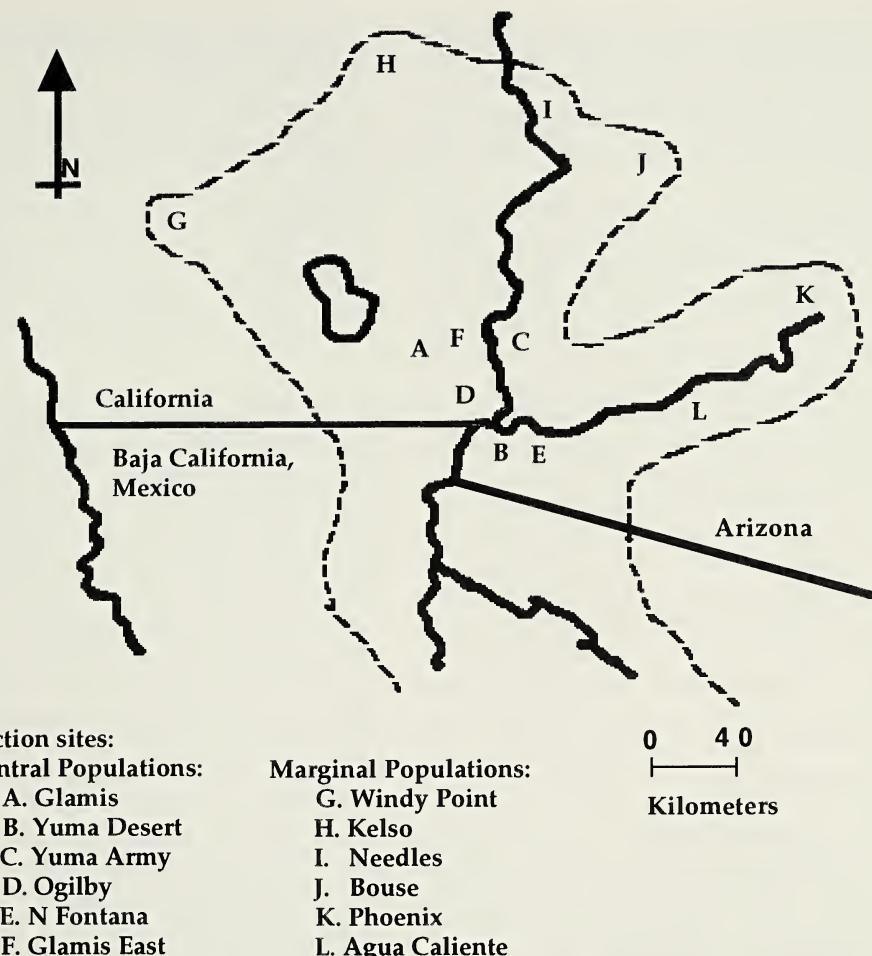
Figure 1.—A partial map of the desert areas of California, Arizona, and Baja California Norte where populations of *Paruroctonus mesaensis* were collected. A proposed range of *P. mesaensis* is indicated by the dashed line.

Collection and electrophoresis procedures.— We collected the scorpions over three years, 1989–1991. *Paruroctonus mesaensis* is easy to collect as it (and all scorpions) fluoresces when illuminated with a ultraviolet light (Sylvania F8T5/BLB). We transported the scorpions alive to the laboratory, froze them with liquid nitrogen, and stored them at −70 °C until electrophoretic analysis.

We electrophoresed five polymorphic and three monomorphic loci from 28 populations. This research was the first allozyme analysis of any scorpion populations, and these eight loci were the only resolvable loci from a screening of 25 enzyme loci on 11 different buffer systems. We assayed a mean of 29 individuals (± 5.7) from each population for each locus. The specific protocols

and other pertinent methodology are described in Yamashita (1993).

Central and marginal population determination.— We determined the geographical center of *P. mesaensis* populations from collection data (Haradon 1983; D. Gaffin pers. comm.; Yamashita 1993) (Fig. 1). We determined the following range extremes: in the north (Death Valley, California); in the south, Cabo Lobos (Sonora, Mexico); in the east (Phoenix, Arizona); and in the west (Windy Point in the Coachella Valley, California). We determined the range center to be located 65 km north of Yuma, Arizona by locating the midpoint between the extreme northern and southern and the western and eastern populations. We designated six populations within a 32 km radius of the range center as

Central populations: Glamis, Yuma desert, Yuma Army, Ogilby, N. Fontana, and Glamis East. We delineated peripheral populations as those nearest to edges of the range. These include Windy Point, Kelso, Needles, Bouse, Phoenix, and Agua Caliente.

Statistical analyses.—We performed two types of analyses to determine if differences between central and marginal populations exist. The first, a method outlined by Weir (1990), tested if heterozygosity differences exist between population types. This design, similar to a split-plot ANOVA, considered variation from five sources: populations, individuals within populations, loci, loci by populations, and loci by individuals within populations. Heterozygotes are entered as 1's, homozygotes, as 0's and the data from each central or marginal populations were pooled. We used electrophoretic data from 20 individuals from each of six central and six marginal populations (120 individuals in each population type) and five loci. We used Weir's analysis because estimates of heterozygosity often exhibit large interlocus variances and non-normal distributions; therefore, many standard parametric tests may be inappropriate (Archie 1985).

Second, we performed standard parametric statistics to determine differences between central and marginal populations. The variables examined were observed average heterozygosity, mean allele number, and percent polymorphism of each population. We calculated these variables using BIOSYS-1 (Swofford & Selander 1989). Observed heterozygosity per locus is the fraction of heterozygous individuals from a given sample for a particular locus (Ferguson 1980; Weir 1990). Observed average heterozygosity is the mean value from all loci. Although heterozygosity values commonly undergo an arcsine transformation, our data did not require such a procedure because most heterozygosity values fell between 0.30 and 0.70, a range that does not require transformation (Sokal & Rohlf 1981).

We used two other indices of genetic variability. Percent polymorphism is the mean number of polymorphic loci in a population. Here, a locus is polymorphic if the frequency of the most common allele is 0.95 or less. The mean number of alleles per locus is the number of alleles at each locus averaged across all loci.

RESULTS

The split-plot ANOVA and standard parametric tests showed the mean heterozygosities

Table 1.—Split plot ANOVA analysis of two population categories (Central and Marginal). This design is taken after Weir 1990.

	df	MS	F-value	P-value
Category	1	3.54	21.60	≤0.001
Individuals within categories	222	0.166	1.01	≥0.437
Loci	4	4.29	26.17	≤0.001
Category × loci	4	1.29	7.86	≤0.001
Error	888	0.164		

from the central and marginal populations were significantly different (Tables 1, 2). The results of the split-plot ANOVA (Table 1) show values from all levels of analysis (populations; individuals within populations; loci; population x loci) were significant ($P \leq 0.001$) except individuals within populations ($P \geq 0.437$). These results establish that central populations are significantly different from marginal ones in heterozygosity. Furthermore, the significant among loci effects suggests that each locus expressed a different pattern of heterozygosity from other loci. Loci within marginal populations were significantly different from loci within central populations, which suggests within each population type (central or marginal), the same locus expressed significantly different heterozygosities.

The mean genetic variability (observed heterozygosity) in marginal populations (0.106 ± 0.025, n = 6) was significantly less than central populations (0.164 ± 0.018, n = 6; t = 3.80, 0.05 ≥ P > 0.01) supporting the central-marginal model. The mean allele number for the central populations (1.73 ± 0.144) was marginally greater (t = 2.21, 0.1 ≥ P > 0.05) than that of marginal populations (1.52 ± 0.095). The mean percent polymorphism for central populations (45.83 ± 6.45) was also marginally greater (35.42 ± 9.41, t = 2.71, 0.05 ≥ P > 0.01).

DISCUSSION

The significant differences between central and marginal populations for allozyme heterozygosity, mean allele number, and percent polymorphism are consistent with the central-marginal model (Brussard 1984). *Paruroctonus mesaensis* is one of the species that fits the predictions of this model; tests of the model using *Drosophila* allozymes failed to exhibit similar patterns (Brussard 1984). In our study, the decrease in genetic variability in marginal populations prob-

Table 2.—A comparison of genetic variability between central and marginal populations. See text for discussion.

	Mean heterozygosity	Mean allele number	% Polymorphism
Central populations			
Glamis	0.153	1.75	37.5
Yuma Desert	0.176	2.00	50.0
Yuma Army	0.136	1.63	50.0
Ogilby	0.167	1.63	37.5
N. Fontana	0.166	1.63	50.0
Glamis East	0.187	1.75	50.0
Mean	0.164	1.73	45.8
SD	0.018	0.144	6.5
Marginal populations			
Windy Point	0.103	1.50	25.0
Phoenix	0.078	1.38	25.0
Bouse	0.131	1.63	50.0
Agua Caliente	0.140	1.50	37.5
Kelso	0.084	1.63	37.5
Needles	0.097	1.50	37.5
Mean	0.106	1.52	35.4
SD	0.025	0.095	9.4
Central *vs* marginal			
t-statistic	3.80	2.21	2.71
P values	$0.05 \geq P > 0.01$	$0.1 \geq P > 0.05$	$0.05 \geq P > 0.01$

ably stems from reduced gene flow or smaller overall population size. Because scorpion dispersal is local, populations at the range margin are less likely to receive migrants from other populations compared to more central populations. Central populations exhibit the highest allele number and percent polymorphism. These populations may maintain higher genetic variability because exchange with other nearby populations is more frequent and population size is generally larger in the center of the range. However, models suggest that a very small effective population size ($n_e < 10$ individuals) is required to reduce significantly the number of alleles per locus within a population (Nei et al. 1975; Rice & Mack 1991).

Some marginal populations (Needles, Bouse, and Phoenix) are geographically isolated from other populations. Needles, north of a mountain range present on either side of the Colorado River, is effectively isolated. The Bouse population exists on the eastern edge of the Cactus Plain, a large sandy region in western Arizona. It is surrounded by rocky habitat and isolated from the nearest population by 40 km. Although Bouse is not separated by a large distance, the intermediate rocky substrate effectively curtails dispers-

al. No *P. mesaensis* were observed in > 30 hours of searching on rocky habitats adjacent to sandy areas (Polis, unpubl. data).

The Phoenix population is the most eastern and one of the most genetically depauperate populations. Emigration into this area probably occurred along the dry river beds of the Salt and Gila rivers. This population relies on unidirectional gene flow since the substrate outside the river bed is a dispersal barrier to the psammophilic scorpion and no populations exist to the east. The low values of genetic variability may be a result of two primary factors: it is a peripheral population with a low population size and receives little gene flow from other populations.

Peripheral isolate formation may have been enhanced by large scale floods in the Holocene (Ely et al. 1993). The Salt and Gila rivers experienced large-scale floods in the last 5600 years (Ely et al. 1993). Periods of minor and major floods were interspersed. These extreme floods may have created expansion corridors for scorpion movement and isolated populations by fragmenting previous habitat.

Although several studies have compared central and marginal populations, a clear trend is not evident (Hoffman & Parsons 1991). Some

report no decrease in genetic variability within marginal populations, e. g., Drosophila allozymes (Brussard 1984) and an annual grass (Rice & Mack 1991). Analysis of dispersal limited animals (frogs) report a decrease in genetic variability among marginal populations (Sjögren 1991). Further research into the properties of marginal populations is warranted because marginal populations, with their insular or peninsular properties, are similar to populations fragmented through man's encroachment upon the environment.

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NATURAL HISTORY, ACTIVITY PATTERNS, AND RELOCATION RATES OF A BURROWING WOLF SPIDER: *GEOLYCOSA XERA ARCHBOLDI* (ARANEAE, LYCOSIDAE)

Samuel D. Marshall[1]:   Department of Zoology & Graduate Program in Ethology, University of Tennessee, Knoxville, Tennessee 37996 USA

ABSTRACT.   Wolf spiders in the genus *Geolycosa* are obligate burrowers and sit-and-wait predators which typically retain their first burrow throughout life. In the present study I document the activity patterns, burrow closure, and relocation rates of an exception to this pattern: *G. xera archboldi* McCrone, endemic to the scrub of central Florida. In census studies of five field plots I document mean relocation rates of up to 3.2% per day. The smaller size/age classes made up the majority of the relocating spiders. I found that individual spiders had their burrows closed on 26 ± 7% of census days. These burrow closures lasted an average of 6.8 ± 0.3 days, with 10% of burrow closures lasting longer than 14 days.

Geolycosa wolf spiders are sessile members of a largely vagrant family. In spite of having evolved the burrowing habit and restricting all activity to the vicinity of the burrow mouth they have retained behavioral features associated with their vagrant ancestors. These traits include vagility and the attachment of the egg sac to the spinnerets. Published accounts of *Geolycosa* indicate that these spiders generally remain with one burrow throughout their lives and relocate seldom (Wallace 1942; McQueen 1983; Conley 1985) or never (McCrone 1963; Miller 1989; Richardson 1990). The only exception to this has been reported by Richardson (1990) for a population of *G. wrightii* in the lakeshore dunes of Michigan which relocates more than once every two weeks.

Studies of *Geolycosa* ecology have assumed that relocation is a rare enough event that burrow abandonment can be equated with mortality (McQueen 1983; Conley 1985). However, there have been no studies explicitly testing this assumption. The purpose of this study is to document the rates of relocation and activity of an apparent exception to the rule of extreme site tenacity in the genus *Geolycosa*. I have also quantified burrow closure across the population. In addition, I will present data on the natural history of a species of special concern in Florida, a state undergoing vertiginous rates of development (Edwards 1994).

[1]Present Address: Department of Zoology, Miami University, Oxford, Ohio 45056 USA

NATURAL HISTORY OF THE MODEL SYSTEM

Study area.—The research presented here was performed at Archbold Biological Station, a private research facility 10 km south of Lake Placid in Highlands County, Florida. The communities represented at Archbold are unique to the southern Lake Wales ridge and belong to a class of habitats referred to collectively as 'scrub' (Abrahamson et al. 1984). In the scrub *G. xera* is limited to areas of open sand. This includes unpaved roads, the open sand of rosemary balds, and patches of open sand in the oak scrub. The naturally occurring areas are created by fire (which consumes the leaf litter) and wind (which moves the accumulated leaf fall). In these patches of open sand *G. xera* may be found in densities higher than any recorded for other *Geolycosa* species (Table 1).

Study organism.—*Geolycosa xera xera* McCrone and *G. x. archboldi* McCrone are endemic to the scrub and sandhill communities of the dry uplands of Highlands, Polk, Lake, Orange, and southern Volusia counties in central Florida (McCrone 1963). The subspecies in the present study, *G. x. archboldi*, is restricted to Highlands County.

Geolycosa xera archboldi digs a distinctive vertical burrow 16.6 cm deep (± 3.2 cm standard deviation, n = 25). Because little silk is used in their construction, these burrows need to be actively maintained in order to persist. A brief rainfall is sufficient to wash burrow mouths closed.

Table 1.—Summary of *Geolycosa* population density estimates for adult females. Adult females are used as this is more widely reported than total population density. Number of samples indicates the number of independent areas or populations studied (modified from Richardson 1990, p. 44).

Species	Spiders/m²	Number of samples	Locale	Source
G. domifex	0.03	1	Ontario	McQueen 1978
G. rafaelana	0.11 ± 0.07	5	New Mexico	Conley 1984
G. wrightii	0.07	1	Michigan	Richardson 1990
G. missouriensis	0.01 ± 0.02	14	Oklahoma	Richardson 1990
G. xera archboldi	0.49 ± 0.25	8	Florida	This study

I saw spiders reopen burrows within minutes of closure due to rainfall or my inadvertently stepping on the burrow mouth. I found that burrow diameter is closely correlated with body size ($P < 0.0001$, $r = 0.92$, $n = 161$) as has been recorded for other *Geolycosa* species (McQueen 1983; Miller & Miller 1984). The foregoing discussion shows how detailed information on the size structure, distribution, and abundance of *G. xera* may be gathered on the basis of burrow characteristics alone.

Geolycosa xera is active year-round. I observed adult females in all seasons, mature males in the fall through spring (see also McCrone 1963) and hatchlings in March through July. Clutch sizes are small (mean ± standard deviation: 24.0 ± 9.0, $n = 5$) compared to an average of 203 for *G. domifex* (McQueen 1978) and 179 for *G. missouriensis* (Richardson 1990). I saw in two successive years (1992, 1993) that the first annual hatchling dispersal from the maternal burrow occurred in mid-to-late March. Hatches were observed throughout the following spring and summer months, but never with the synchrony of the first hatch of the year. I saw no obvious climatological correlates of the dispersal event to explain this synchrony. March is during the dry season in Florida, and the weather is fairly constant. The long breeding season, coupled with year-round activity, the size-class distributions noted above, and observations of captives I have held in the lab for extended periods lead me to believe that *G. xera* matures in 18–24 months. This is similar to published accounts for other *Geolycosa* species (Wallace 1942; McCrone 1963; McQueen 1978; Miller & Miller 1987).

METHODS

Activity and relocation rates.—I established five 2.0 × 2.0 m unenclosed census plots in patches of open sand in scrubby flatwoods. These census plots were all at least several meters apart in distinct and separate sand patches. I censused these plots every other day from 6 March until 3 May 1991. Using dial vernier calipers, at each census I measured the burrow mouth diameter of new burrows to the nearest 0.1 mm and marked them with a numbered surveyor's flag. I also noted whether previously flagged burrows were open or closed. I estimated the mean length of burrow closure periods from those burrow closures which were initiated and terminated within the census period. Extended burrow closure was assumed to be initiated and terminated by the spider. I calculated the percent of censuses in which the individual burrows were closed by dividing the number of censuses the burrow was closed by the total number of censuses for those individual burrows which were both active at the end of the census period and censused at least 10 times. As these data were taken from five defined census plots I report the means and standard deviations as calculated from census plot means.

For the estimates of relocation rates I only considered those burrows found open after the first 14 days of the census period (this minimized the counting of reopened burrows as new, see results below). I also did not count hatchlings in order to avoid inflating relocation rates by including recruitment.

Characterization of relocating individuals.—I enclosed a naturally-occurring habitat patch approximately 12.5 m² with sheet metal flashing. This site was chosen for the study of size-classes and movement as it had a larger population of *G. xera* (approximately 100 individuals) than the census patches used above. In order to examine the relative sizes of relocating *versus* resident individuals, I arbitrarily divided the total number of new burrows for the period (10–18 July 1990) into four size classes and compared these data
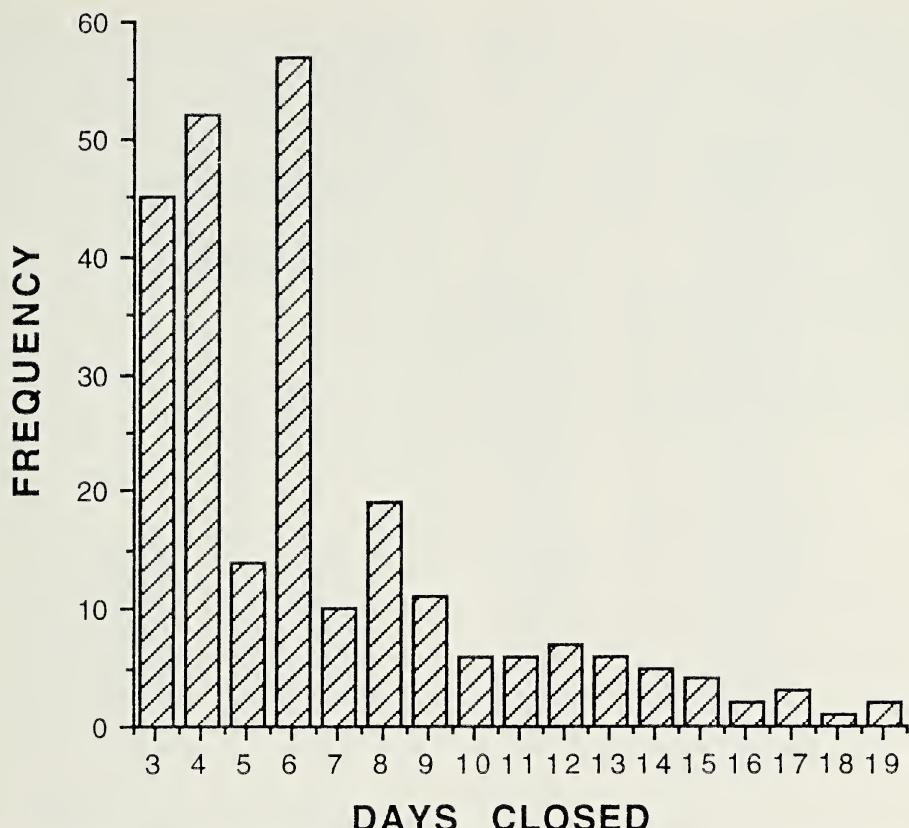
Figure 1.—Duration of burrow closures for a population of marked *Geolycosa xera archboldi* burrows censused every other day in five 4.0 m² open census plots at Archbold Biological Station, Highlands County, Florida (*n* = 250 burrow closures).

to the four size classes of the long-term residents active on 14 July.

RESULTS

Activity and relocation rates.—I found that 90% of burrow closures lasted 14 days or less (Fig. 1). The duration of burrow closures was 6.8 ± 0.3 days (mean ± SD, *n* = 5). Individually, spider burrows were closed 26.0 ± 7.0% (*n* = 5) of

Table 2.—Summary of relocation rates of *Geolycosa xera archboldi* at Archbold Biological Station in five 4.0 m² census plots, 22 March to 19 April 1991.

Site	Density (spiders/m²)	Mean daily relocation rate (%)
1	7.20	1.0
2	4.75	1.4
3	2.54	3.2
4	2.04	1.8
5	1.41	2.5

census days. The proportion of new burrows found at each census was 2.0 ± 0.9% per day (*n* = 5, Table 2). This represents my estimate of the relocation rate.

Characterization of relocating individuals.— New burrows belonged predominately to the smaller size classes (Fig. 2). Larger, and thus older, spiders are less likely to change burrow sites than the smaller, younger individuals.

DISCUSSION

Geolycosa xera exhibits unexpectedly high relocation rates for a fossorial spider. Whether the rates I measured in the spring remain as high throughout the year is unknown. However, these results indicate that *Geolycosa* wolf spiders may not all be as sedentary as previously thought.

Given the energetic cost implicit in burrow construction and the risk of predation involved in leaving the security of a burrow, it would be predicted that these spiders would only move in extreme circumstances. Dispersal is assumed to

Figure 2.—Composition of a population of *Geolycosa xera archboldi* at Archbold Biological Station. 'Relocating' (*n* = 36) are from new burrows found at daily censuses 10–18 July 1990. 'Residents' (*n* = 73) denotes burrows open on 14 July 1990 (exclusive of 'Relocating').

be risky; and therefore, many studies of dispersal and migration have looked for an adaptive explanation for animal movement (Southwood 1962; Gaines & McClenaghan 1980; Johnson & Gaines 1990). There are no data on the cost of burrow construction in *Geolycosa*; however, there are data which can give us an indication. Culik & McQueen (1985) studied activity patterns and metabolic rates in *G. domifex* and found that movement on the surface elevated metabolic rates 220%, and moving up and down the burrow elevated rates 1780%. As burrow construction involves moving sand up the burrow to the surface, burrow construction should be even more costly than moving up and down the burrow unburdened. Janetos (1987) has documented that there is an inverse correlation between relocation rates and web cost in web spiders. While the evolutionary scenario for web-spiders may not extend

to burrow-building spiders, a burrow is likely to represent a long-term investment in a site.

The higher rates of relocation for the younger spiders I found are consistent with patterns reported by other workers (Conley 1985). Why younger spiders are more likely to relocate than older individuals is unknown. I do not feel that relocation to find a better microhabitat site is responsible given that all size/age classes of *G. xera* may be found in close proximity to each other. It may be that stochastic events (e. g., burrow collapse) or territorial interactions with neighbors may be responsible.

I have no data on foraging and relocation rates for *G. xera*, but have observed several possible stochastic mechanisms to explain burrow abandonment. I have seen excavations at the burrow mouth which I attributed to predation attempts which may have been the cause of subsequent

burrow abandonment due to damage to the fragile burrow. I have twice observed that ants invading the burrow to pirate prey elicit a spectacular and immediate response: the spider bolts from the burrow and jumps up into the nearest vegetation. I have three times observed attacks by neighboring conspecific burrow holders on smaller individuals engaging in burrow maintenance behaviors. I have also seen burrow abandonment correlated with encroaching leaf litter.

The burrow of *Geolycosa* wolf spiders may represent both a prison and refuge. Given the cost of construction and maintenance, these spiders may have evolved a foraging strategy and life history centered on the burrow more like those other obligate fossorial spiders, the mygalomorphs, and very unlike their peripatetic confamilials. It seems probable that the obligate fossorial habit of *Geolycosa* evolved in abiotically stringent habitats such as sand dunes. However, *Geolycosa* can make up for this restriction to relatively barren and prey-depauperate sandy habitats by foraging for a longer period each day (vagrant lycosids in the scrub are nocturnal). The burrow permits individuals to shuttle between the thermally extreme conditions at the surface while foraging and the more moderate thermal environment of the burrow. The evolution of the fossorial habit also allowed an eresid to invade barren sand dunes in the Namib desert (Lubin & Henschel 1990).

Geolycosa xera archboldi has the most restricted range of any known *Geolycosa* wolf spider. It lives in a specific microhabitat within an endangered ecosystem (Edwards 1994; Marshall 1994). While the densities it achieves at suitable sites can be quite high, unless the habitat is periodically burned, populations decline as patches of open sand are covered with leaf litter. *Geolycosa x. archboldi* cannot tolerate any leaf litter covering the burrow mouth, and will abandon any burrow covered with leaf fall. *Geolycosa xera* is an excellent indicator species of the quality and health of patches of scrub in Florida's beleaguered uplands habitats: it is active year-round, sensitive to burn frequency, and identifiable on the basis of burrow characteristics and locale alone. Populations persist at far smaller patches of scrub than do endemic vertebrates (e. g., Florida scrub jays).

ACKNOWLEDGMENTS

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OBSERVATIONS OF HABITAT USE BY *SARINDA HENTZI* (ARANEAE, SALTICIDAE) IN NORTHEASTERN KANSAS

Stephen R. Johnson[1]: Division of Biology, Ackert Hall, Kansas State University, Manhattan, Kansas 66506 USA

ABSTRACT. During the mid-autumn of 1993 and spring through summer of 1994, I sampled tallgrass prairie in northeastern Kansas to determine habitat use, distribution and population dynamics of the ant-like jumping spider *Sarinda hentzi* (Banks). This species was not detected in any censused area of tallgrass prairie until early October 1993, when large juvenile specimens were found in a density of 0.54 individuals/m² on inflorescences of Indian grass (*Sorghastrum nutans* (L.) Nash.) in a biennially burned watershed. During the following spring, 0.6 adults/m² were found on Indian grass panicles in a four-year burned watershed and 0.4 adults/m² were located on Indian grass inflorescences in another biennially burned watershed. By mid-summer 1994, this species was no longer found on Indian grass and only very small juveniles were found on various *Carex* and *Juncus* species at the margins of wetlands.

Spiders which mimic ants have a large suite of morphological and behavioral adaptations (McIver & Stonedahl 1993). Many of the ant-mimicking spiders belonging to the families Clubionidae and Salticidae avoid predation by their mimicking deception (Cutler 1991). The feeding behaviors, food preferences and general biology of selected ant-like salticids have been well documented by Jackson (1982, 1986) and Wing (1983); however, there is little available information on habitat use by North American ant-like salticids (Duffy 1978; Cutler, pers. comm.).

In northeastern Kansas, the family Salticidae is most commonly represented by the genera *Metaphidippus* and *Phidippus* (Fitch 1963). Two species of ant-like salticids, *Sarinda hentzi* (Banks) and *Synomosyna formica* Hentz, may also be common (Fitch 1963; S. Johnson, pers. obs.); however, virtually nothing is known about the natural history of these species in this region (B. Cutler, pers. comm.).

The purpose of this study was to 1) investigate habitat preferences, 2) estimate population densities and 3) record seasonal population dynamics of *Sarinda hentzi* in the tallgrass prairie of northeastern Kansas because *S. hentzi* may be the most frequently encountered ant-like salticid

[1] Present address: Department of Biology, Virginia Commonwealth University, Richmond, Virginia 23284-2012.

of the tallgrass prairie in northeastern Kansas (S. Johnson, pers. obs.).

METHODS

Research was conducted at the Konza Prairie Research Natural Area (KPRNA) located approximately 10 km south of Manhattan, Kansas (39°08'N, 96°35'W). This site is a member of the Long Term Ecological Research Network established in 1981 (Callahan 1984). Fire is an important component in the maintenance of tallgrass prairie where, in the past, natural fires were common events (Pyne 1982; Abrams et al. 1986). Today, fire is a frequent management practice in tallgrass prairie (Anderson 1972; Blankespoor 1987). All prescribed fires occurred on KPRNA in mid-Spring (late March through April). In early June and mid-August through mid-October 1993, I conducted a survey to ascertain distribution and habitat preferences of *Sarinda hentzi*. Samples were collected by taking 50 sweeps while walking along parallel transects in hilltop plateau, midslope and wetland margin sectors of tallgrass prairie (Cutler 1971). Three separate samples were collected for each distinct zone by sweeping three parallel transects in each of the three distinct zones (Fig. 1). Samples were taken in three annually burned, two biennially burned, two 10-year and two 20-year burned watersheds. The number of spiders captured per sample was converted to an estimated density of spiders/m² by taking the number spiders/sample and divid-

Figure 1.—Positions of sweep samples taken in hilltop, midslope and wetland margin zones of tallgrass prairie. Each replicate consisted of 50 sweeps at the inflorescence level. Duplicate samples in the hilltop and midslope zones were taken at the level of basal leaves approximately 0.3 m above the ground.

ing it by the number of inflorescences/m² in the habitat where the sample was collected. The density of Indian grass and big bluestem (*Andropogon gerardii* Vitman) culms and inflorescences was determined by taking 50 0.1 m² quadrat samples in each location where sweep samples were taken. Where *S. hentzi* was frequently encountered, sweeps of single infloresences were made to determine the spider density per individual inflorescence. This single inflorescence data was also used as an index of the estimated density of individuals/m². To determine if *S. hentzi* was present elsewhere in the habitat, separate sweep samples were taken among basal leaves of the grasses. Captured spiders were counted after each individual sweep and subsequently released back onto grass infloresences.

In 1994, sampling began in early May and continued until early August. Samples were taken in the same manner as described for 1993; however, the sampling procedure was expanded to include two additional four-year burned watersheds.

RESULTS AND DISCUSSION

In 1993, a year with rainfall amounts 33 cm above a 30-year mean (KPRNA weather data, unpubl.) no *S. hentzi* were collected in any watershed until early October. Otherwise, from June to early October, the most commonly collected spiders on inflorescences of Indian grass (*Sorghastrum nutans*) in annually and biennially burned (1992 burned) watersheds were *Marpissa pikei* (G. & E. Peckham) (Salticidae) (0.45 ± 0.18

individuals/m² in June, 0.27 ± 0.15 ind./m² in October), *Thiodina puerpura* Hentz (Salticidae) (0.32 ± 0.19 ind./m² in June, 0.18 ± 0.09 ind./m² in October) and *Tibellus duttoni* (Hentz) (Philodromidae) (O.56 ± 0.12 ind./m² in June, 0.32 ± 0.2 ind./m² in October). In these watersheds, Indian grass inflorescences occurred in an average density of 40.3 ± 8.2/m² and the total density of Indian grass culms was 59.6 ± 12.2/m². Where big bluestem was dominant, it occurred in a density of 73.6 ± 14.3 culms/m² with 68.3 ± 8.4 inflorescences/m². In adjacent 10 and 20 year burned watersheds both Indian grass and big bluestem were more patchily distributed and occurred in less dense and often mixed stands. There, Indian grass inflorescences occurred in a density of 12.5 ± 2.2/m² and big bluestem inflorescence densities were comparable. Also, broad leaved forbs were more common. In early June, *Metaphidippus galathea* (Walckenaer) and *Phidippus clarus* Keyserling were the most common species collected. In early October, inflorescences of big bluestem were being used as perches by *Phidippus audax* (Hentz) (0.3 ± 0.19 ind./m²) and *P. apacheanus* Chamberlin & Gertsch (0.12 ± 0.08 ind./m²). No *S. hentzi* were found in annually, 10- or 20-year burned watersheds.

Beginning in early October 1993, large juvenile *S. hentzi* (~10 mm in length) were collected in a density of 0.54 ± 0.12 individuals/m² on inflorescences of Indian grass in the mid-slope transects of a biennially burned watershed (Fig.
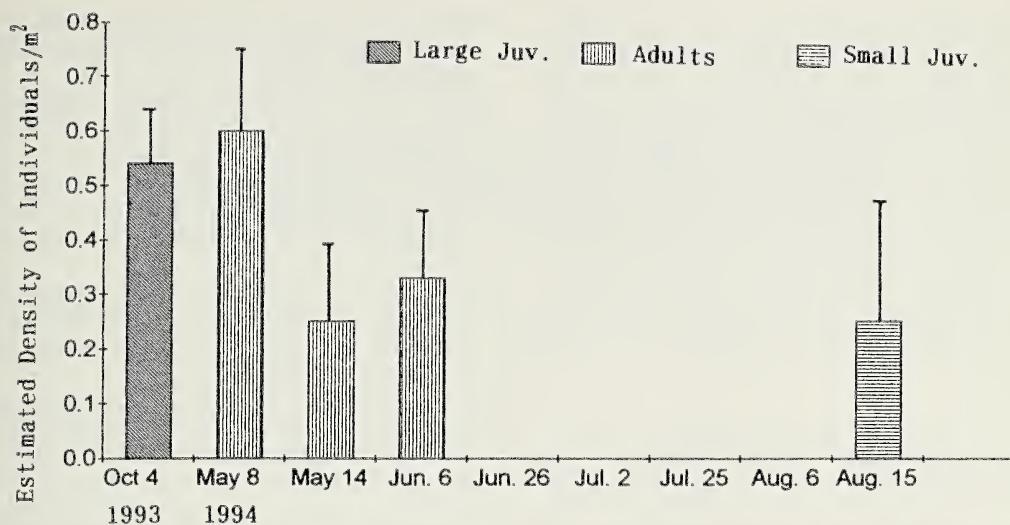
Figure 2.—The estimated density of *Sarinda hentzi* individuals/m² in early October 1993 and from 8 May through 15 August 1994. Vertical bars represent one standard error of the mean.

2). These juveniles were occasionally found in groups of two or three per inflorescence in pure stands of Indian grass. By mid-October, no *S. hentzi* juveniles were found in this area.

In early May 1994, a year with a more normal level of rainfall, *S. hentzi* adults were found in a density of $0.6 \pm 0.15/m^2$ on old inflorescences of Indian grass in a four-year burned watershed (Fig. 1). By mid-May, in the same watershed, the number of adults in Indian grass inflorescences had dropped to 0.25 ± 0.14 individuals/m² (Fig. 2). Sweeps of grass blades around these inhabited Indian grass canes failed to capture any *S. hentzi*. By the end of May, adult *S. hentzi* were no longer found on Indian grass inflorescences in this watershed.

In a biennially burned watershed located several kilometers south of the four-year burned watershed, 0.35 ± 0.19 adult *S. hentzi*/m² were found in Indian grass inflorescences on the hilltop sampling position in early June (Fig. 2). These individuals were sympatric with the same three grass-inhabiting species: *M. pikei*, *M. puerpura* and *T. duttoni*. Twice in the early June sampling I captured *M. pikei* being eaten by *T. duttoni*; however, I never observed *S. hentzi* being preyed upon by any of the other mentioned species.

By late June all species were in reduced densities which were concentrated farther downslope from the sites sampled in early June. By mid-July, these grass-inhabiting species were most concentrated at the margins of wetlands among *Carex annectens* Bicknell, *C. hystericina* Muhl.,

Eleocharis erythropoda Steudel and *Juncus torreyi* Coville where the combined density of plant culms was $86.8 \pm 23.5/m^2$. Here, I found the *M. pikei* and *T. duttoni* in densities of more than 0.7 individuals/m² each. Conversely, I found only one adult *S. hentzi* in 100 sweeps. By mid-August I found no adult *S. hentzi* but did capture tiny juveniles (1.5–2 mm in length) in a density of 0.25 ± 0.2 ind./m² (Fig. 2). A similar density of juvenile *S. hentzi* was found in the margin of the wetland basin of the four-year burned watershed where the high density of adults had been found during the preceding May.

From these observations, I hypothesize that *S. hentzi* is a grass inhabiting species somewhat like *Marpissa pikei* in northeastern Kansas but may be more restricted in habitat. Because *S. hentzi* was only found in intermediate burn frequencies and generally absent from annually-burned and long-term unburned areas, it may be avoiding potentially greater competition from higher density spider populations in annually-burned prairie, following the pattern of many other grass-inhabiting spiders in long-term unburned prairie (Weaver 1987; Usher 1988; S. Johnson, unpubl. data). With this habitat specificity, *S. hentzi* may also be an indicator of environmental quality (Clausen 1986). Also, it seems either to be prone to large fluctuations in population density or is sensitive in some way to sweep net sampling. Some evidence for this such sensitivity comes from population density dynamics of sympatric spiders. For example, while numbers of adult *S.*

hentzi dropped precipitously from early May to early June, numbers of *Metaphidippus galathea* and *Tibellus duttoni* in the same area remained fairly constant over the same period of time (0.27 $\pm$ 0.18 and 0.66 $\pm$ 0.21 ind./m² respectively, in early May; 0.21 $\pm$ 0.06 and 0.59 $\pm$ 0.20, respectively, in early June). Furthermore, while experimental manipulation and statistical analysis were not part of this descriptive study, these observations may help formulate appropriate questions to design experimental work on arthropod habitat preferences in the tallgrass prairie ecosystem.

ACKNOWLEDGMENTS

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LABORATORY STUDIES OF THE FACTORS STIMULATING BALLOONING BEHAVIOR BY LINYPHIID SPIDERS (ARANEAE, LINYPHIIDAE)

Gabriel S. Weyman: School of Biological Sciences, University of Southampton, Bassett Crescent East, Southampton, SO9 3TU, UK

ABSTRACT. Linyphiid spiders were tested individually in the laboratory in order to assess possible factors stimulating the onset of ballooning behavior. An air flow chamber was used for many of the tests. Air movement was found to be an important stimulus for initiating both the climb to a prominent position and subsequent take-off attempts. After instigation of pre-flight behavior by an initial air flow stimulus, climbing continued in still air, though take-off attempts generally ceased in the absence of further air movement. Neither circadian rhythmicity nor darkness were found to prevent exhibition of ballooning behavior at night. Length of time spent attempting to take-off appeared to be a factor in reducing a spider's response to the stimuli causing ballooning behavior.

Ballooning is the term commonly used to describe aeronautic dispersal using wind drag on threads of silk for lift, as exhibited by several families of spiders. At certain times of the year these spiders take to the air en masse, though there are lower numbers ballooning throughout the year (Freeman 1946; Sunderland 1991; Weyman et al. 1995). There must be innate factors governing which spiders will balloon and at what stage during their lifetime, possibly with environmental factors adjusting the likelihood of its occurrence at a particular time (see Weyman 1993 for a review). However, occurrence of this critical component of spider population dynamics is finally driven by individual behavior in response to immediate stimuli.

Although several studies have been carried out to investigate when, and under what meteorological conditions, spiders take to the air (e.g., Greenstone 1990; Vugts & van Wingerden 1976; Thomas 1993), very little work has been done on the immediate factors that stimulate spiders to initiate and cease the behaviors that result in flight. The current investigation explored some of the factors that may be responsible by observing individual spiders subjected to a variety of stimuli in the laboratory. This set of basic experiments assessed the importance of each stimulus, to detect those which are worthy of more intensive investigation.

Air flow is an important factor in ballooning because it provides the source of power for spider flight (Humphrey 1987; Suter 1991, 1992). It would seem likely, therefore, that air movement might be the stimulus that elicits ballooning behavior (taken here to include the pre-flight behaviors). It is well documented that spiders will not take off in wind speeds over 3 m/s (Richter 1970; van Wingerden & Vugts 1974; Vugts & van Wingerden 1976; Greenstone 1990). There is also limited evidence that spiders do not balloon at night (Bishop 1990). Suction trap data (Sunderland unpubl.) show extremely low numbers of spiders caught at night, even between high day catches (maximum night catch of 5, compared with a maximum day catch of 178). There are two possible explanations for this: 1) that meteorological conditions at night are not suitable for ballooning; 2) that pre-flight behavior (climbing to a high point and attempting to take-off) ceases at a certain time in response to the light-dark cycle or an endogenous circadian rhythm.

Laboratory experiments were carried out in an air flow chamber, similar to one used by Legel & van Wingerden (1980), to determine whether air movement was a sufficient stimulus to elicit climbing and take-off behavior. Further experiments were carried out to determine whether climbing and take-off behavior require continuous stimuli, or whether they continue after a short initial stimulus, in the manner of a fixed action pattern (FAP) (Manning 1979).

The hypothesis that ballooning does not occur
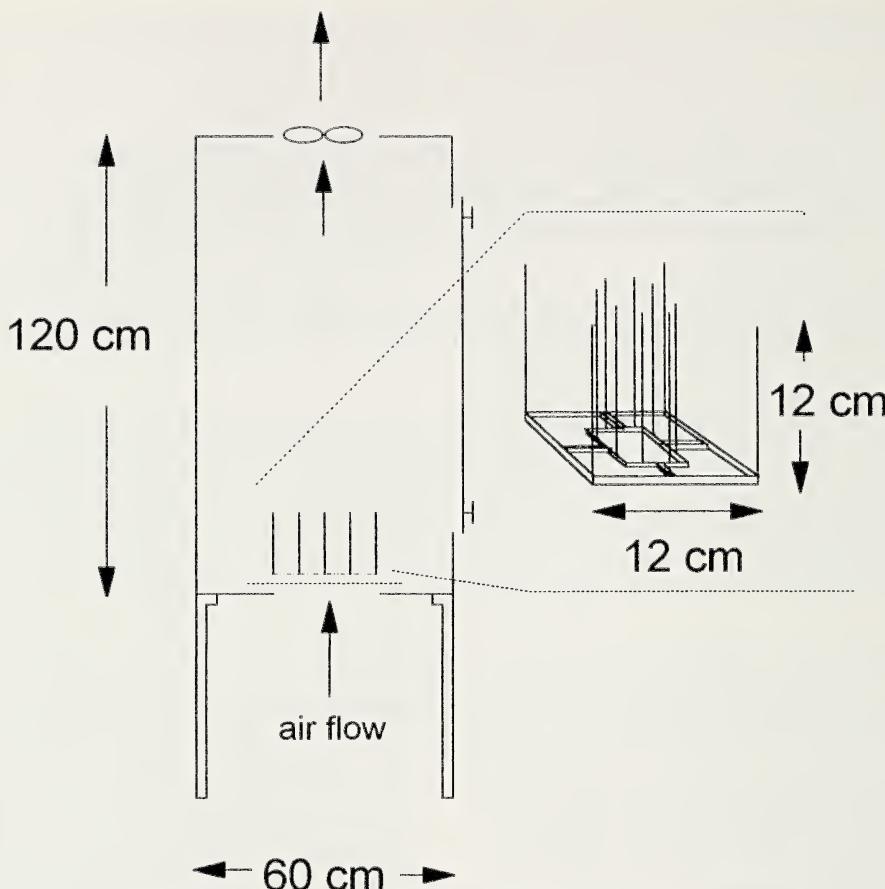
Figure 1.—Schematic diagram of the laboratory air flow chamber.

at night for behavioral reasons was tested in the laboratory. Evidence for an endogenous circadian rhythm was sought by subjecting spiders to ballooning stimuli during the night. Other spiders were tested for ballooning behavior in effective darkness. Duration of the ballooning behavior was also assessed as a possible factor limiting a spider's responsiveness to the stimuli presented.

METHODS

Collection of spiders.—*Erigone* spp. were collected as required from unsprayed grassland on a farm 20 miles north of Southampton, UK, by Dietrick vacuum insect net (D-vac). Samples were sorted on the day of collection and spiders were placed individually in 3 cm diameter Petri dishes with a small piece of moistened filter paper to avoid desiccation. *Erigone* spp. were identified live under a binocular microscope before testing,

or preserved in 70% alcohol after testing awaiting identification. The spiders were not identified to species, but only *E. atra* (Wid.) and *E. dentipalpis* (Bl.) were found at the collection site in population samples during 1991 and 1992. These two species are expected to exhibit very similar behaviors as they have virtually identical life-cycles, niches and habits (De Keer & Maelfait 1988). Storage and testing of spiders were carried out in a controlled environment room at 18 °C ± 2, relative humidity 70% ± 10, L16:D8 cycle (approximately in phase with external conditions), except where stated otherwise.

The air flow chamber.—The laboratory air flow chamber used here was an acrylic sheeting ("perspex" or "Plexiglas") box 120 cm high, with a 55 × 60 cm base (Fig. 1). A suction fan in the top (Rotron Inc. Whisper Fan WR3A1, 230V AC, 12W) drew air through a 12 × 12 cm square opening in the center of the base, covered with metal gauze as a support. White netting covered

the whole of the base to aid viewing and a wooden climbing frame with 12 cm uprights was placed over the opening. The updraft at 1 cm above base level in the frame was 0.57 ms^{-1} ± 0.01 (measured with a Solomat MPM 500e hotwire anemometer, 950 readings logged at 5 s intervals). Take-off within the confines of the chamber was not normally possible but pre-flight behavior could be observed and recorded easily. This chamber was also used by Weyman et al. 1994, 1995).

Erigone spp. are ground-dwelling spiders which do not normally climb (C. J. Topping pers. comm.), except when motivated to balloon. Having climbed to a prominent position, prior to take-off, a spider assumes the position known as "tip-toe" (Richter 1970), with legs extended and abdomen raised, and releases silk until the drag on the length of silk is sufficient to lift the spider from the substrate, or possibly until some higher optimal threshold is reached. In an alternative take-off behavior, referred to here as "dropping" (after Jones 1994), the spider drops a short way on a thread, while a second thread provides wind-drag for lift.

Factors eliciting ballooning behavior.—*Airflow as the stimulus for climbing in the laboratory:* The individual Petri dishes containing spiders were maintained in a large plastic container with high r.h. (≈ 100%) achieved by putting a small amount of water in the base. Testing for climbing behavior was then carried out in the laboratory air flow chamber. To observe the effect of airflow on the behavior of spiders previously in calm conditions, individual spiders were first observed in still conditions, then with air movement over them. Individual Petri dishes containing spiders were placed in the center of the climbing frame, with the fan off. A piece of plasticine ("modeling clay") was attached to the lid of the Petri dish, attached to a cotton thread running out through a hole in the top of the chamber. The door of the chamber was then closed and the lid gently lifted off the Petri dish by pulling the cotton thread. The spider was observed for three minutes before the fan was switched on. Observations then continued for a further three minutes. Wind speed just above the open Petri dish was found to be 0.0 m/s with the fan off, and fluctuated between 0.0–0.1 m/s with the fan switched on (measured with a Solomat MPM500e hotwire anemometer). Three separate experiments were carried out, with groups of 10, 29, and 29 spiders respectively.

Air flow as the stimulus for take-off behavior in the laboratory: To determine the necessity of continuous air flow as a stimulus for ballooning behavior, 16 spiders were individually subjected to a short stimulation/disturbance by collection in a hand aspirator, and placed into the climbing frame in the chamber with the fan off. Each spider was observed for three minutes. Climbing and "tip-toe" behaviors were recorded. After a short rest period the same spiders were re-tested in the same way, but with the fan turned on.

To further examine the effect of changing air flow stimulus, individual spiders were placed into the climbing frame, with the fan off, and observed for 44 minutes with the fan alternately turned on or off at ten minute intervals, starting with a still period. The occurrence of several behavioral categories was recorded: moving or stationary at base level (assigned the term "ground"); climbing the uprights ("climbing"); activity at the top of the uprights ("top active"); inactivity whilst at the top of the uprights ("top inactive"); take-off attempts by the dropping method ("dropping"); take-off attempts by the tip-toe method ("tip-toe"). The experimental time was divided into 30 s periods, and assessment of behavior was by a standard presence or absence (1/0) method during each 30 s. The most advanced behavior towards take-off was noted for each 30 seconds. This method gave four interfaces of changing conditions for each spider tested and would show any possible effects of previous conditions on subsequent ballooning behavior. Ten minute intervals were used to allow valid assessment of individual behavior types over a large number of 30 s periods between each interface, with the final four minutes to allow any change after the final interface to become clearly apparent. Sample intervals of 30 s were chosen by experience, for logistic reasons. Four individuals were tested in this way, each constituting an independent repetition.

Factors limiting response to initiation stimuli.—*Testing for endogenous rhythms:* Testing was carried out in a portable ballooning chamber, similar to the one described above but modified with a plywood base and a DC fan (Papst multifan 4132, 9 cm, 12 V DC, 5W), giving an equivalent air flow. The chamber was situated in a room which did not have environmental control facilities, but variations in ambient humidity and temperature over the experimental period were not expected to affect the results. The room was illuminated naturally during the day and by a
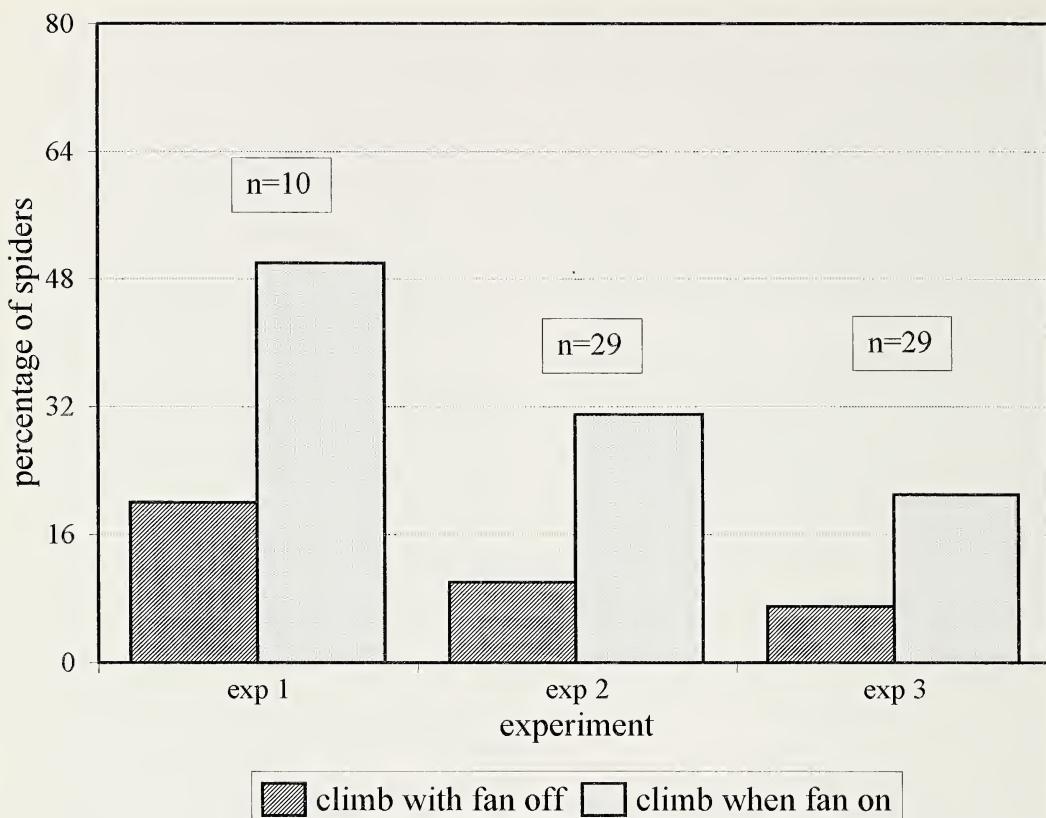
Figure 2.—The percentage of spiders climbing during the test period with the fan off, and the additional number climbing after the fan was switched on.

100 W incandescent source during dark hours only while testing was in progress. The results gained could be used to assess the necessity for more controlled conditions.

Thirty-two spiders were individually tested for pre-aeronautic behavior within three minutes of being placed via hand aspirator onto the base of the wooden frame. Climbing and "tip-toe" behaviors were recorded over a three minute period. The spiders were tested once during the daytime, once during darkness, and once again in the following light period. This was repeated for each spider on the subsequent day.

Testing for limitation of ballooning response in darkness: To test whether darkness limits response by spiders to a ballooning stimulus, linyphiids were collected by hand aspirator as they attempted to take-off from fences and grass at the field collection site. The spiders were placed individually in Petri dishes then placed into an opaque box. The spiders were kept in the box for approximately three weeks before being assessed for ballooning behavior.

Testing was carried out in an open arena with a fan blowing across it, where infra-red lighting was available, and where take-off was possible. Spiders are not thought to be sensitive to infra-red light (M. F. Land pers. comm.). Light intensity at floor level, where the spiders were placed, was 0.05 μ Einsteins/m²/s (readings taken with a Li-Cor model Li-185B photometer). Ten spiders from the opaque box were individually tested for three minutes. Climbing, "tip-toe", and take-off behaviors were recorded.

Testing for limits to duration of time spent attempting take-off: To assess the duration of ballooning behavior, individual spiders were initially given six min in the laboratory ballooning chamber, with the fan on, to initiate ballooning behavior. Presence or absence of "ground", climbing, "dropping" and "tip-toe" behaviors was determined over one min periods. If a spider exhibited ballooning behavior then it was allowed to continue until it descended to ground level and remained there for six consecutive min, with no indication of further climbing. The test
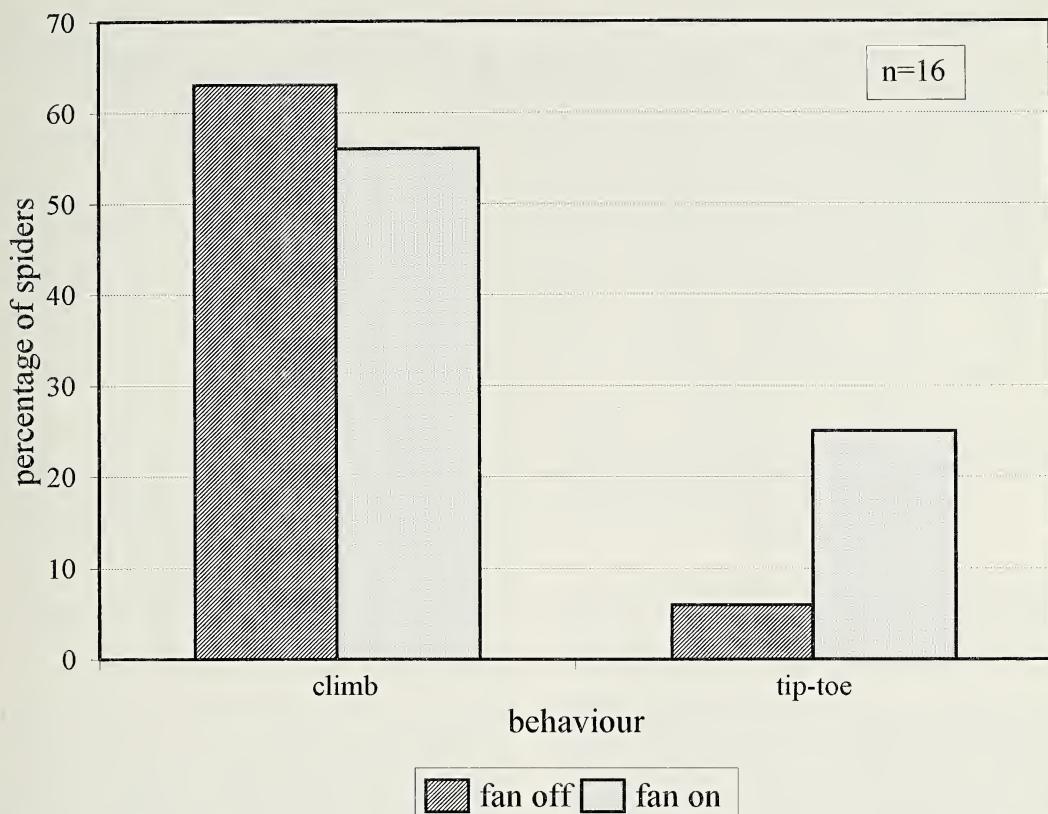
Figure 3.—The behaviors exhibited in the ballooning chamber within three minutes of release with the fan either on or off, after the initial stimulation by hand aspiration.

was then terminated. Individuals were re-tested to determine whether cessation was permanent or temporary. Six min was allowed to give added assurance of a spiders intent to start or stop ballooning, compared to the usual three min period of other experiments. This was important because the experiment was designed to measure accurately time spent showing ballooning behavior for individual spiders, rather than being a qualitative comparison between different groups or conditions, as made in experiments with the shorter time period. A total of 45 tests was carried out on 21 spiders.

RESULTS

Factors eliciting ballooning behavior.—*Air flow as the stimulus for climbing:* A small proportion of spiders climbed with the chamber fan switched off. They may have responded to air movement lower than the threshold of the measuring equipment, or to disturbance as the Petri dish lid was

removed (Fig. 2). The onset of air flow elicited climbing for most of the spiders, however.

Air flow as the stimulus for take-off behavior: After aspiration, as many of the 16 spiders climbed with the fan off as when it was on (Fig. 3), with no significant difference between the tests ($G = 0.1$, $df = 1$, $P > 0.05$). Although climbing behavior often ensued following the initial stimulus, "tip-toe" behavior was rare and only increased after further stimulation (Fig. 3), though the observed difference was not significant ($G = 2.3$, $df = 1$, $P > 0.05$). The limitations of the G-test in this context, where repeated measures are made on the same subjects, are recognized. It is used here as a simple indicator of the level of differences between tests.

In the second set of experiments, where four spiders were tested individually for 44 min each, pre-flight climbing again continued in the absence of the air stimulus (Figs. 4–7). This may suggest the existence of a FAP for ballooning behavior. "Tip-toe" behavior was again largely
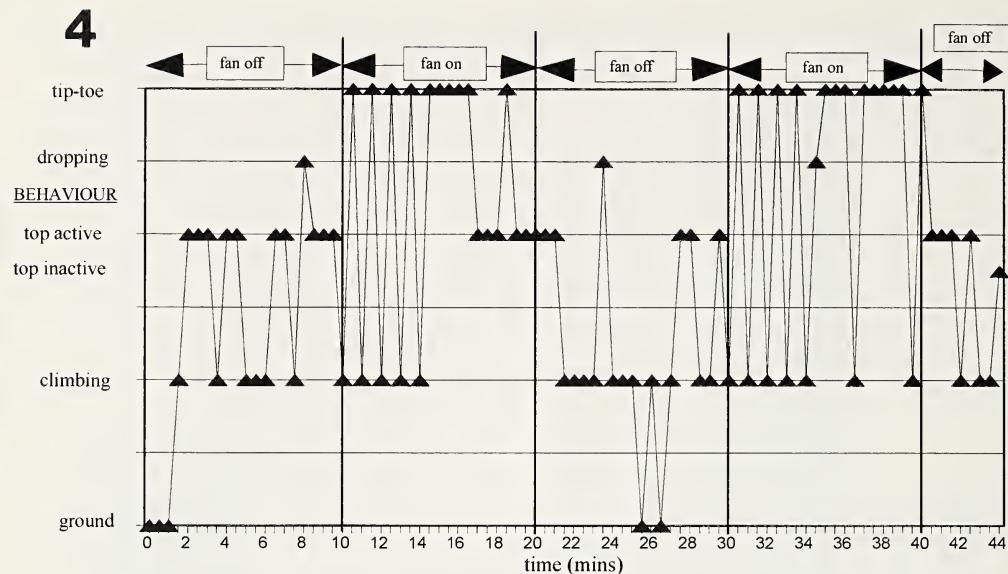
Figure 4.—The effect of air movement on pre-ballooning behavior for spider A. Behavior recorded in 30 second periods with fan on or off.

dependent on air flow, but did occasionally appear to be exhibited in its absence. This was difficult to assess, however, because spiders did not seem to fully extend into the "tip-toe" position unless the silk thread released was being pulled by the updraft. All four spiders tested showed marked differences in their behavior when the fan was switched on or off. Most no-

ticeably, a much higher proportion of time was spent tip-toeing with the fan on, and more time was spent climbing with the fan off (Table 1). Only spider B showed signs of ending ballooning behavior during the 44 min period (Fig. 5).

Factors limiting response to initiation stimuli.—*Endogenous rhythms:* Spiders showed climbing and "tip-toe" behaviors at all test times
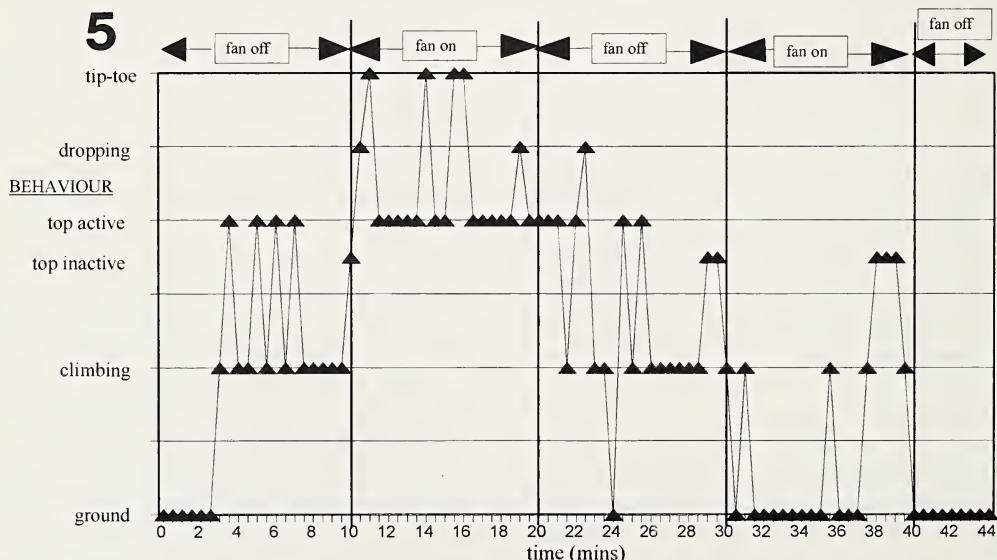
Figure 5.—The effect of air movement on pre-ballooning behavior for spider B. Behavior recorded in 30 second periods with fan on or off.

Table 1.—The proportion of the total assessment points at which each behavior was exhibited by each of four spiders.

Behavior	Spider A		Spider B		Spider C		Spider D	
	Fan on	Fan off	Fan on	Fan off	Fan on	Fan off	Fan on	Fan off
Tip-toe	0.575	0.000	0.100	0.000	0.500	0.083	0.550	0.021
Dropping	0.025	0.042	0.050	0.021	0.000	0.021	0.150	0.042
Top active	0.150	0.396	0.375	0.167	0.400	0.271	0.225	0.354
Top inactive	0.000	0.021	0.075	0.063	0.000	0.000	0.000	0.021
Climb	0.250	0.458	0.100	0.438	0.100	0.542	0.075	0.563
Ground	0.000	0.083	0.300	0.313	0.000	0.083	0.000	0.000
	40	48	40	48	40	48	40	48

(Table 2), with no significant differences between times (*G*-test, $P > 0.05$, $df = 2$), suggesting that there is no endogenous circadian rhythm limiting ballooning behavior at night. Statistical limitations of the *G*-test apply, as stated above.

Effect of darkness: Ten spiders were tested under infra-red light. Six of these showed ballooning behavior: three of the six showed climbing and "tip-toe" behavior, and three climbing and "dropping". One of the tip-toeing spiders became airborne.

Duration of time spent attempting to take-off: Of the 21 spiders tested, ten showed ballooning behavior on at least one occasion. A total of 16 ballooning periods was observed. Time to cessation of ballooning behavior ranged from 3–267 min. The mean duration ± SD was 48 min ± 73. Six of the 16 ballooning periods were in retests of spiders that had shown ballooning behavior on a previous occasion, suggesting that respites are only temporary. There was no in-

Table 2.—Percentages of spiders showing pre-ballooning behavior during the day and at night in the laboratory ballooning chamber. (ns = not significant) (dark at 1930 h).

Testing time	% climbing	% tip-toeing	Number tested
Replicate 1			
1800–1930 h	53%	44%	32
0000–0140 h	72%	44%	32
1100–1300 h	56%	32%	32
G-statistic	2.6 (ns)	1.4 (ns)	
Replicate 2			
1400–1600 h	63%	25%	32
2220–2400 h	63%	41%	32
0940–1140 h	48%	23%	31
G-statistic	1.8 (ns)	2.8 (ns)	

dication of individuals having set durations for ballooning behavior periods, one spider showing a range of 8–129 min to cessation.

DISCUSSION

Air flow was indicated as an important initial stimulus in the initiation of ballooning behavior. In the experiment to determine whether air flow is the stimulus for climbing it could be argued that the extra time allowed more spiders to exhibit climbing during the second three min period, with the fan on. However, many spiders were observed to have an immediate and strong climbing response as soon as the fan was turned on, indicating the importance of air flow as a stimulus.

When spiders were tested under infra-red lighting, to which they are thought to be insensitive, ballooning behavior could still be instigated. Thus darkness was not found to limit ballooning. Spiders tested for ballooning tendencies at different times showed no indication of an endogenous circadian rhythm limiting ballooning after dark. These results do not necessarily mean that spiders regularly balloon at night, but they certainly suggest that there is no endogenous reason why they should not, due to circadian rhythms or photo-responsiveness. Meteorology is implicated as the major factor limiting ballooning at night. Conditions may simply not be suitable for take-off, even if spiders are attempting to fly at night. Farrow (1982, 1986) found spiders flying in large numbers at night in the upper air. However, this was facilitated by a nocturnal temperature inversion which actually prevents take-off as the surface air cools. The spiders, therefore, took off during the daylight hours, and remained aloft until re-inversion of the temperature gradient the next day. Observations might reveal spiders attempting to take-off at

Figure 6.—The effect of air movement on pre-ballooning behavior for spider C. Behavior recorded in 30 second periods with fan on or off.

night in greater numbers than previously recorded, but not succeeding.

It appears that, once initiated, ballooning behavior is carried to completion (take-off, when possible) or until some limit is reached (indicated here as temporal or energetic), even if the stimulus is removed. This suggests that some sort of fixed action pattern (FAP) acts to maintain the behavior for some time after initiation, in the absence of further stimulus. An alternative explanation could be that a lack of air movement provided the stimulus for continuation of the behavior when the fan was switched off. However, lift from an updraft is necessary for take-off so it would be expected that spiders should stop the pre-ballooning behavior and descend, or at least become less active to conserve energy and lower their visibility to predators such as
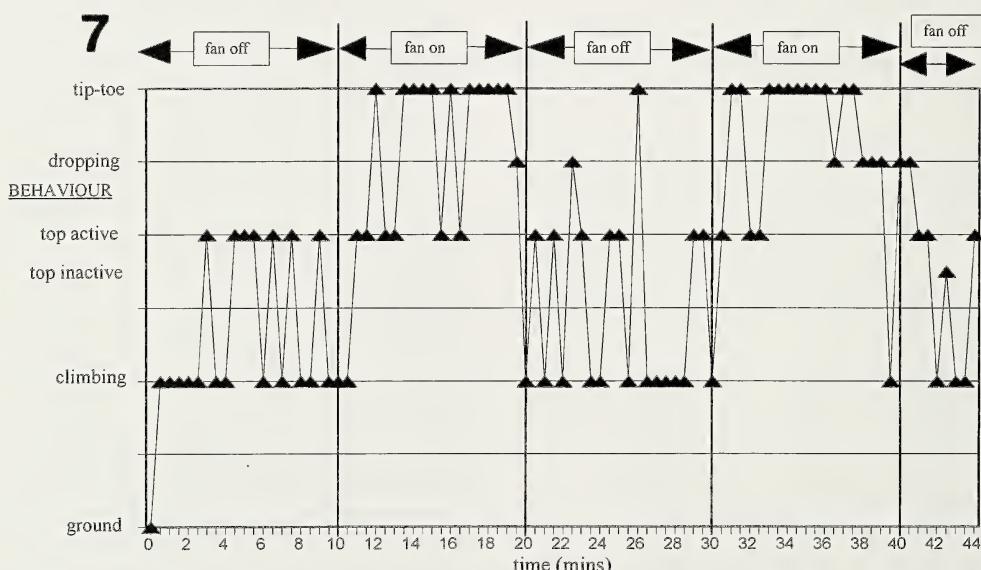

Figure 7.—The effect of air movement on pre-ballooning behavior for spider D. Behavior recorded in 30 second periods with fan on or off.

birds, if ballooning attempts became unsuccessful.

The reason for the FAP type activity observed here is unclear. As mentioned above, spiders normally occupying a niche on or near the ground under dense vegetation must be risking much higher chances of predation by climbing to a prominent position and moving around. It is possible that a FAP to continue the behavior allows for natural changes in the airflow above the vegetation, so the spiders do not continually climb and descend as windspeed rises and falls, thereby possibly missing suitable conditions for take-off attempts.

The temporal shut-off suggested here, in the experiment to determine the duration of ballooning behavior, is not representative of the field, where conditions are not continually suitable or stimulating and there may be enforced breaks in ballooning, as well as the voluntary respites suggested here. Also, in the laboratory flight was not possible, only constant attempts. A period of just 10 minutes of take-off attempts may equate to several successful flights in the field. Thomas (1993) found wide variation in the time between flights in spiders observed ballooning in the field, ranging from 1–66 min, with a modal interval of 1 min before flight was resumed. These times are taken between successful flights and, of course, are subject to changes in conditions for stimulus and flight.

Results here suggest that spiders show highly variable duration of ballooning bouts, interspersed with temporary rest periods which, in combination with variable numbers of flights per day and variable flight distance (Thomas 1993) means that individuals will travel extremely variable distances on a day when conditions are suitable for ballooning. Dispersal will be very high, as will the variety of habitats sampled, compared to a group all travelling the same distance in the same direction and landing more or less in a group downwind from the start point.

It would be extremely useful, in terms of modelling spider spatial dynamics, to observe the full temporal and spatial range of different ballooning behaviors, and distances travelled in flight (and, indeed, cursorily) for a large number of individual spiders in the field. However, it is virtually impossible to follow a spider in flight for more than a short distance, or to follow one through the vegetation. It would also be valuable to discover the full range and nature of the stimuli involved in ballooning in the field, though

expensive equipment and many observation hours are required for accurate meteorological readings to be taken within and above a crop in combination with behavioral observations. Some work of this nature has been undertaken, by Thomas (1993), van Wingerden and Vugts (1974), and by the current author (unpubl.), for example, though the complex interactions between meteorological factors have tended to obscure results pertaining to stimulation of spider ballooning behavior.

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CHANGES IN BIOMASS OF PENULTIMATE-INSTAR CRAB SPIDERS *MISUMENA VATIA* (ARANEAE, THOMISIDAE) HUNTING ON FLOWERS LATE IN THE SUMMER

Douglass H. Morse: Department of Ecology and Evolutionary Biology, Box G-W, Brown University, Providence, Rhode Island 02912 USA

ABSTRACT.   Penultimate-instar crab spiders *Misumena vatia* foraging on goldenrod *Solidago* spp. in late summer gained mass slowly, averaging 0.8 mg/day, and usually did not molt into the adult stage before the end of the summer. In contrast, adults gained mass rapidly at this site, averaging 8.8 mg/day, taking larger prey and taking them more often than penultimates. The penultimates' prey consisted primarily of small flies, bees and wasps, and overlapped broadly with those of the adults, but did not include the most important resource of the adults, bumble bees, upon which the adults registered most of their gain. Penultimates captured prey biomass at only one-tenth the rate of the adults, and one-third the rate of adults per unit body mass.

Most studies of foraging animals have focused on adults (Morse 1980; Pyke 1984; Stephens & Krebs 1986), even though preadult stages may occupy the majority of many species' lifetimes. Proponents argue that this approach addresses the stage that contributes directly to reproduction, permitting the most ready estimation of fitness (see Lewontin 1978; Maynard Smith 1978). However, foraging events earlier in the life-cycle may affect one's success as an adult (Morse 1980; Skelly & Werner 1990; Fraser & Gilliam 1992), and lack of early success may result in many individuals not even surviving to the adult stage (e. g., Forrest 1987). Thus, information is needed on immature stages to compare with adult success, to determine how well adult foraging success describes foraging success in general (see Stein & Magnuson 1976; Sih 1982), and to establish how foraging repertoires vary over a range of sizes and ages.

Different life-cycle stages may vary in their proficiency at capturing a given kind of prey. This pattern is clearly illustrated by the success of the semelparous crab spider *Misumena vatia* Clerck (Thomisidae) at capturing bumble bees (*Bombus* spp.), which only adult females can subdue (Morse, unpubl. data). This prey is critical to fitness – without bumble bees, adult females seldom if ever gain enough mass to lay their single clutch of eggs (Fritz & Morse 1985).

Stages lacking similarly profitable prey will grow slowly, and molting and maturation may be greatly extended (Levy 1970). In addition to dangers resulting from increased time spent as a juvenile, slow growth may make such individuals vulnerable to critical seasons that can act as bottlenecks. For instance, many species of spiders do not overwinter as adults (e. g., Schaefer 1977), including *Misumena* (Morse unpubl. data). To evaluate growth patterns of a stage without access to extremely profitable prey, I gathered data on the activity patterns, prey capture, and rate of gain in mass of penultimate female *Misumena*, which cannot capture bumble bees. The results permitted me to compare the success of these penultimates with adult female *Misumena*, whose foraging and growth patterns my colleagues and I have studied in detail (Morse 1979, 1981, 1986, 1988; Morse & Fritz 1982, 1987; Fritz & Morse 1985; Kareiva, Morse & Eccleston 1989). For direct comparison, I also gathered similar data on the small number of prereproductive adult females present in the study area at the same time. Most adult females had already laid their eggs and were guarding them at that time (Morse 1987).

I conducted this study during late summer on *Misumena* that frequented goldenrods *Solidago* spp., the dominant native flowering plants in eastern North America at this time of year. Goldenrods are the principal foraging sites for *Misumena* at this season (Morse 1981, 1993). In the absence of an "ideal" prey for the penultimates, comparable to bumble bees for the adults, one may predict a relatively slower growth rate from the penultimates than from adults.

CHARACTERISTICS OF *MISUMENA*

The semelparous crab spider *Misumena vatia* (Thomisidae) has a life cycle of one year or more.

These spiders frequent flowers that attract large numbers of their insect prey. Typically, adult females lay their single clutch of 75–350 eggs during mid- or late summer, with extremes of early July to early September (Morse & Fritz 1982; Fritz & Morse 1985). Females guard their eggs in nests constructed from leaves, often until the young emerge nearly a month later (Morse 1987). Young overwinter as immatures in the litter, usually as third to sixth instars, but with less frequent penultimates and second instars. Some individuals probably overwinter more than once, but I have no evidence that they overwinter as adults. To date I have not recovered in the following spring any of the more than 300 marked adults (over a period of 15 field seasons) that did not lay eggs in the fall (Morse unpubl. data). [Neither have I recovered in the following spring any of the 1400 + egg-layers I have studied (Morse 1994) during this time.] Following wintering, these spiders hunt on flowers for insect visitors. Females subsequently grow rapidly if they find hunting sites that attract many large insect prey, sometimes increasing as young adults by as much as an order of magnitude (40 mg to 400 mg) within as little as two–three weeks (Fritz & Morse 1985). Penultimate females range from about 18 mg to 75 mg or more (Holdsworth & Morse in press), and can be readily separated from adults by the absence of red dorsolateral stripes on their abdomens (Gertsch 1939). Males are strikingly smaller than females, seldom exceeding 7 mg, and averaging 3–5 mg (Holdsworth & Morse in press).

METHODS

I carried out this study in a one ha field in Bremen, Lincoln County, Maine. The field is covered by a variety of grass species, with considerable numbers of forbs scattered throughout. During late July and August 1981, when this study was conducted, goldenrod was the dominant flowering forb. The principal species of goldenrod, blooming in sequence, were *Solidago juncea*, *S. canadensis*, and *S. rugosa*. They will be considered collectively for the purposes of this study. Clonal in nature, these goldenrods typically exhibit a clumped distribution, with 10–75 flowering stems per site in the study area. This site is described in further detail elsewhere (Morse 1979, 1981).

I used 45 immature female *Misumena* in this study, which, at 18–34 mg, were almost certainly all in the penultimate instar. [In another study,

all 49 females of this size range captured in the field and subsequently reared through to their next molt assumed adult condition at 31 mg or more, with a mean of 54.7 mg ± 12.5 SD (Holdsworth & Morse unpubl. data).] These penultimates were added to the study as found, thus Day 1 of observations was not the same for all individuals.

I gathered data simultaneously on a sample of eight prereproductive adult females, all of these individuals I could find in the study area at this time. The small sample size of adults deserves note. Numbers of these individuals were extremely low in the study area, and the failure of additional small, prereproductive adult females to appear during the study period strongly suggested that very little, if any, recruitment occurred from the pool of penultimate females into the adult population.

Spiders were initially given a unique number, placed on the abdomen, using indelible ink. They were then weighed on a Kahn Electrobalance, returned to their sites on goldenrod and censused for presence, location, and prey capture at least every two hours during the daytime for periods of up to two weeks. Repeat weighings were made for 13 of the penultimate individuals and six of the adults at intervals averaging three–four days. Visits at two–hour intervals ensured that I recorded nearly all of the diurnal prey that the spiders captured (Morse 1979, 1981). Any nocturnal captures, which are infrequent on goldenrod and confined to moths taken by adults (Morse 1981), could be detected by the presence on the following morning of carcasses still being fed on or recently discarded (Morse 1981).

The penultimate spiders were divided into three groups on the basis of the information gathered upon them: 1) weighed two (3), three (7) or four (3) times and observed for several days (5–12 days); 2) weighed once and observed more than one day (3–11 days); and 3) weighed once and observed for a single day. As a result, some of these individuals provide more information than others. Six of the adult females met the criteria of Category 1 (3–13 days) and the other two of Category 2 (2–6 days). Adults in Category 1 were weighed two (1), three (4), or four (1) times.

Insect prey were recorded and assigned to group (usually order, but species in case of principal prey) and size category. Routine weighings of fresh specimens of these species (Morse unpubl. data) permitted rough estimates of prey biomass at time of capture. Although ingested biomass

Table 1.—Characteristics of penultimate and adult female spiders. First two variables drawn from entire sample of individuals; last three variables drawn from sample that was weighed two or more times.

	Penultimates			Adults		
	$\bar{x} \pm SD$	N	Range	$\bar{x} \pm SD$	N	Range
Time between first two moves (days)	4.0 ± 3.0	24	1–11	5.3 ± 3.6	8	1–13
Distance of moves (cm)	50.0 ± 52.4	24	10–200	40.8 ± 15.8	4	25–60
Gain in mass (mg/day)	0.8 ± 0.5	13	−0.2–24	8.8 ± 6.2	6	−0.8–22.3
Gain in mass (%/day)	3.0 ± 2.4	13	−0.9–10.3	9.1 ± 5.5	6	−1.0–16.8
Time observed (days)	9.0 ± 2.0	13	7–12	6.5 ± 3.6	6	3–13

would have permitted a more precise measure of prey intake, it was impossible to capture and weigh the free-ranging prey before the spiders caught them. However, an earlier study (Morse 1979) demonstrated that adult female *Misumena* extracted very similar proportions of the smallest and largest prey items exploited by spiders in this study (57.5% of the *ca.* 4 mg syrphid fly *Toxomerus marginatus* and 57.1% of *ca.* 150 mg bumble bees *Bombus* spp.). Therefore, use of the wet masses of prey species should provide an acceptable estimate for comparisons. Biomass captured (estimated cumulative wet mass of all prey) was divided by total days of observation to determine the rate at which spiders obtained resources. I determined gains in mass from the spiders I weighed more than once. Rates of gain were established by dividing the total change in mass between the first and last weighings by the days elapsed.

RESULTS

Penultimate spiders weighed twice or more and observed several days initially weighed 25.4 mg ± 6.1 SD; those weighed once and observed more than one day weighed 24.9 mg ± 5.3 SD; and those weighed and observed one day weighed 23.2 mg ± 4.5 SD. These three groups did not differ in mass ($H = 0.891$, $df = 2$, $n = 45$, $P > 0.5$ in a Kruskal-Wallis one-way ANOVA). Therefore, I treated them as members of a single group for each variable about which they yielded data.

Gains of penultimates were slow, though variable, averaging 3% of their body mass per day (Table 1). In these individuals the mean increase amounted to 0.8 mg/day. At this rate they would gain an average of 24 mg/month, one month being the maximum possible time remaining with substantial numbers of flowers in bloom as hunt-

ing sites and temperatures favoring prey activity. Two of the 13 individuals even lost a small amount of mass (0.4, 0.9% of initial mass/day), falling from 23 to 22 mg over nine days, and from 24 to 22 mg over 11 days, respectively. The remainder gained from 0.5 to 10.3%/day, with only three of the individuals increasing over 1.0 mg/day. The two fastest gainers increased from 23 to 42 mg in eight days, and 23 to 40 mg in 11 days, respectively. Original mass and subsequent gain of this group of 13 spiders were not significantly correlated ($r_s = -0.316$ in two-tailed Spearman Rank Correlation Coefficient, $n = 13$, $P > 0.2$).

The penultimates' gains in mass can be compared with those of the adult females occupying the same flowers (Table 1). The adults, which weighed nearly four times as much as the penultimates (94.2 mg ± 29.8 SD, $n = 8$), gained mass 10 times more rapidly than penultimates and, as a function of gain per unit mass, three times more rapidly than penultimates (Table 1). These differences were both significant ($P = 0.01$ in two-tailed Mann-Whitney U Tests). Two of these adult females more than doubled their original mass, in 7 and 13 days, respectively; none of the penultimates exhibited such large relative gains. [Original mass and subsequent gain were not correlated in this sample ($r_s = -0.236$ in a two-tailed Spearman Rank Correlation Coefficient, $n = 6$, $P > 0.2$).]

This difference in uptake of mass mirrored the adults' superiority in total numbers of prey captured per unit time ($G = 6.89$, $df = 1$, $P < 0.01$ in a G-Test: Table 2) and size of prey captured ($P < 0.01$ in a Mann-Whitney U Test: Table 2). Notwithstanding the pronounced difference in gain of mass by adults and penultimates, they did not differ significantly in either the frequency with which they changed goldenrod inflorescences (Table 1; $P > 0.7$ in a two-tailed Mann-

Table 2.—Prey captured on goldenrod by penultimate and adult female spiders.

Prey	Penultimate (n = 45)			Adult (n = 8)	
	Mass (mg)	Number caught	Total (mg)	Number caught	Total (mg)
Toxomerus marginatus (Syrphidae)	4	13	52	1	4
Other small Diptera	8	6	48	2	16
Medium Diptera	15	1	15	2	30
Small bee	10	4	40	3	30
Small wasp	10	4	40	3	30
Butterfly	15	1	15	0	0
Moth	125	0	0	1	125
Bumble bee (*Bombus* spp.)	150	0	0	4	600
Spider (Salticidae)	10	0	0	1	10
Total	—	29	210	17	845
Total spider days		228		53	
Capture/day (mg)		0.92		15.9	
Size of item (mg)		7.2		49.7	

Whitney *U* Test) or in the distance that they moved at such times (Table 1; $P = > 0.5$, same test). Prey species taken by penultimates and adults overlapped broadly, but the penultimates did not capture any bumble bees, the major source of prey gain for the adults.

DISCUSSION

Although the critical data set is small, adult and penultimate female spiders differed markedly in their energetics during the late summer. The low rate of gain in mass suggests that many of the penultimate instars (probable minimum of 9 out of 13) would not reach the size at which they would likely molt into the adult stage (mean = 55 mg, minimum = 31 mg: see Methods) while foraging on goldenrod. Even those that grew large enough to molt to the adult stage would be very unlikely to grow large enough to lay a clutch of eggs. I have never found *Misumena* laying a clutch in the field if they weighed less than 114 mg (Fritz & Morse 1985; Morse unpubl. data). That few penultimates did molt into adults during this period is further suggested by the small numbers of prereproductive adult females present at that time (n = 8) and the extremely low rate at which additional small prereproductive adults were found over the study period.

This growth pattern of penultimates contrasts with the small cohort of adults observed at this time, which gained considerable mass as a result of capturing bumble bees, a prey that lies beyond the size range available to the penultimates.

Adults in another study on goldenrod also gained mass rapidly (Morse 1981), a trait observed earlier in the summer on other species of flowers as well (Morse 1981; Fritz & Morse 1985). The penultimates' slow growth also contrasts with the success observed for early-instar *Misumena* on goldenrod, which recruit regularly onto this flower from their nests (Morse 1993), and frequently increase in mass several fold as a result of feeding on the small Diptera that frequent goldenrod flowers.

In this northerly clime, penultimates have at most a month of feeding time left before temperatures decline abruptly (early to mid-September), and an even shorter time before the last goldenrods senesce (late August–early September). Following the disappearance of the last goldenrod flowers in early September, only scattered asters (*Aster* spp.) remain, such that the opportunities for successful hunting decline markedly for these flower-frequenting individuals. These factors further decrease the possibility that many of them will molt into the adult stage before the end of the season. Their slow rate of growth will therefore relegate them to a second overwintering, which potentially entails further mortality. These spiders will, however, presumably be among the first to molt into the adult stage during the following spring and early summer and the first to lay their eggs in midsummer. Had they realized a rate of gain in body mass proportional to that of the adults on goldenrod (also see Morse 1981 for comparable suc-

cess rates of adults on goldenrod), many would probably have molted into the adult stage at this time. Even this increase would, however, have consigned them to a close race to produce a clutch of eggs by the end of the season. Since I have, to date, no evidence of adult *Misumena* surviving over winter, increase in size and subsequent molt would have likely obviated an opportunity to reproduce. If they did succeed in laying a clutch, it, too, might be vulnerable to cold damage. If such clutches do reach the hatching stage, the success of the earliest instars is open to question. Second-instar young are extremely vulnerable to starvation, at least earlier in the season (Vogelei & Greissl 1989; Morse 1993). Further, the numbers of adult males at this season become extremely low (Holdsworth & Morse in press), so the possibility of an unfertilized clutch among late-developing adults at this season is high. Thus, in spite of the dangers of the impending winter, the penultimates' slow gains in mass on goldenrod may be more advantageous than they first appear. The penultimates' slow rate of gain may even allow them to accommodate for a natural "bottleneck" of the seasons. Their failure to change sites more rapidly or to move farther than adults at these times (Table 1) does not suggest that they are responding at this time to a perceived food shortage in a way characteristic of most animals, including adult *Misumena* (Morse & Fritz 1982).

Although the exact basis for molt into the adult stage is not known for *Misumena*, nutrition, size and growth rate are very likely to be critical environmental factors in terrestrial arthropods (Blakely 1981; Forrest 1987; Nijhout 1994). The marginal size (for molt) and slow growth rate characterizing these penultimates should be strong factors prolonging the onset of molt.

The results do not justify arguing at this time that the penultimates deliberately ration their rate of intake. However, as suggested by both Miyashita (1969) and Wise (1976), low availability of food late in the season may facilitate the delay of maturity in species that do not overwinter as adults.

Some arthropods are intrinsically programmed to suspend maturation in the latter part of summer. For example, the pitcher-plant mosquito *Wyeomia smithii* does not proceed into the last instar under decreasing photoperiods, which signify the return of winter conditions before the mosquito can complete its reproductive period

and its offspring can reach an overwintering stage (Istock 1981).

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REDESCRIPTION OF THE SCORPION
CENTRUROIDES THORELLI KRAEPELIN (BUTHIDAE)
AND DESCRIPTION OF TWO NEW SPECIES

W. David Sissom: Department of Biology & Geosciences, WTAMU Box 808, West Texas A & M University, Canyon, Texas 79016 USA

ABSTRACT. The Central American scorpion *Centruroides thorelli* Kraepelin 1891 is redescribed, based on examination of the type material and additional specimens now available. It is readily diagnosed by its smaller body size, mottled color pattern, the shape of the female pectinal basal piece, and the shape of the male telson and subaculear tubercle. Two new species related to *C. thorelli* are also described, one from the lowlands of Guatemala and the other from mountainous areas in southern Tamaulipas and northern San Luis Potosi in Mexico.

Centruroides thorelli was described on the basis of six specimens collected by Stoll in Guatemala (Kraepelin 1891). The species was accepted as valid by Pocock (1902), who mentioned several additional specimens in the British Museum, also originating from Guatemala. In Hoffmann's (1932) monograph on the scorpions of Mexico, a new series of specimens was reported from Chiapas, Mexico. The thorough description given by Hoffmann and study of the types of *C. thorelli* provided enough evidence to determine that his specimens are not referable to this species. Other researchers have also misidentified the species (Ocaranza 1926; Diaz Najera 1966); in particular, Moreno (1939, 1940) described two subspecies from Cuba, *C. t. cubensis* and *C. t. aguayoi*, which are now considered synonyms of *C. guanensis* Franganillo.

Francke & Stockwell (1987) studied specimens from Guatemala, Belize, and Costa Rica and suggested that at least two forms were present among their samples, but opted to place their Costa Rican specimens under *C. thorelli* by giving a very general description. The present study confirms their original suspicions by recognizing two distinct species, *C. thorelli* from high elevations in Belize and Guatemala and a new species from lowlands in Guatemala. The Costa Rican material, which was not available, awaits further study. A second new species is described from the central Mexican states of Tamaulipas and San Luis Potosí, representing a form that is widely separated geographically from other members of the complex. Whether this disjunction is real, or is the result of inadequate collecting in the intervening areas, remains to be seen.

Centruroides thorelli Kraepelin
Figs. 1–9

Centrurus thorelli Kraepelin 1891: 124; 1899: 89–90.
Centruroides thorelli Pocock 1902: 22, pl. 5, figs. 2, 2a–c; *nec* Hoffmann 1932: 304–307, figs. 77, 78 (misidentification); 1938: 319 (misidentification); *nec* Ocaranza 1926: 77 (misidentification); *nec* Moreno 1939: 73–74 (misidentification); *nec* Diaz Najera 1966: 111, 113 (misidentification); 1975: 4, 18 (misidentification); Stahnke & Calos 1977: 112, 114 (part); Moritz & Fischer 1980: 324; Francke & Stockwell 1987: 17–18, figs. 48–56, 100 (part); *nec* Armas, et al. 1992a: 6 (misidentification); *nec* Armas 1992b: 131–132, fig. 4 (misidentification).
Rhopalurus testaceus thorelli Meise 1934: 32, 34.

Type data.—Adult male lectotype, 1♂ paralectotype, 4♀ paralectotypes (designated by Francke & Stockwell 1986) from Guatemala, Stoll (leg.); housed in the Zoologisches Museum, Berlin (Cat. No. ZMB 7633); examined.

Distribution.—Known only from Guatemala.

Comparative diagnosis.—*Centruroides thorelli* has been a rather distinctive, but poorly understood, member of the genus. The original description (Kraepelin 1891) and the treatment by Pocock (1902) point out its uniqueness among *Centruroides* by being the only species with eight rows of denticles on the cutting edge of the chela fingers that has the dorsum mottled, rather than striped. In fact, most other cuticular surfaces are also mottled. Its small size (*ca.* 35–40 mm), low pectinal tooth counts (less than 17), and the bilobed telson in the male have also been cited in comparing it with other *Centruroides* (Pocock 1902). Unfortunately, subsequent researchers have used the name inappropriately because un-
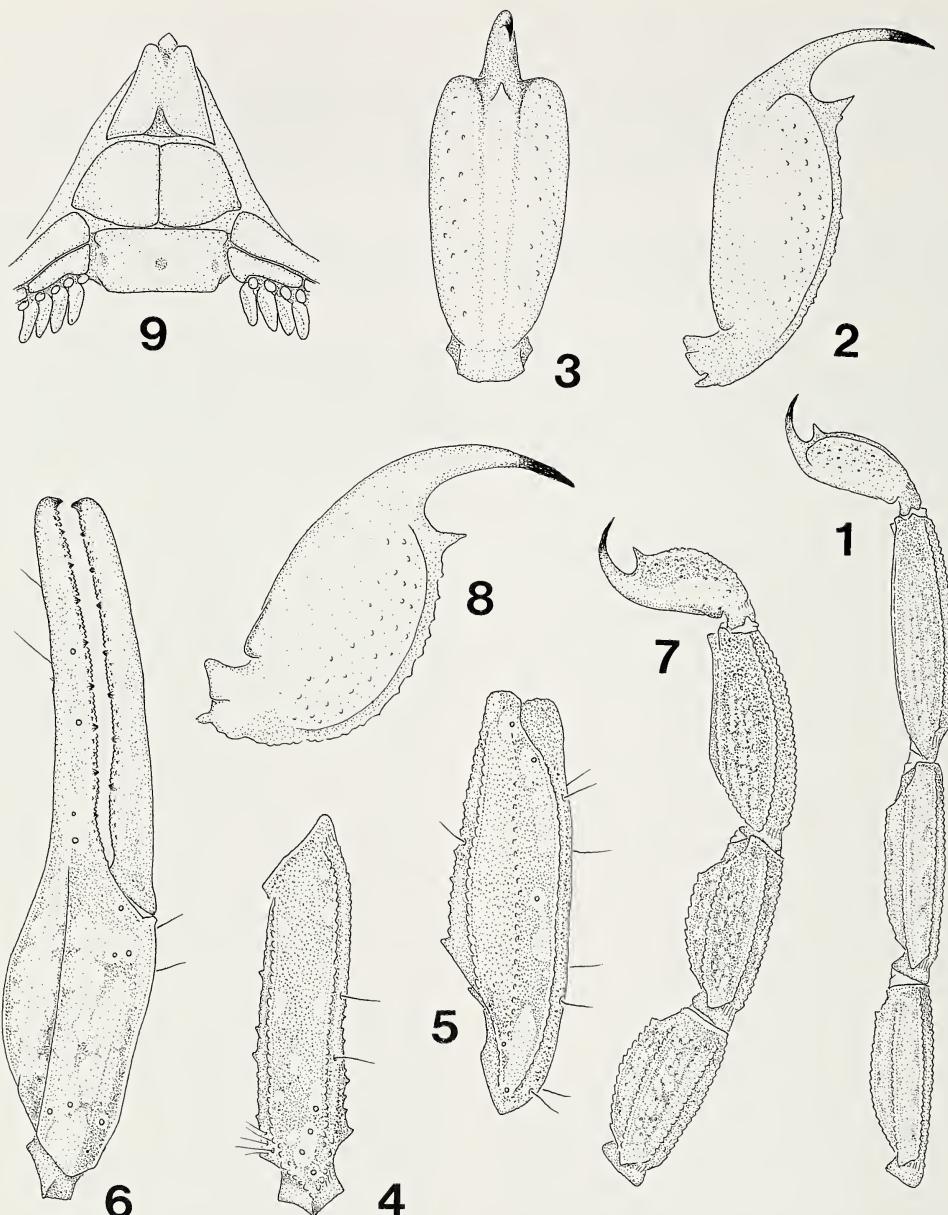
Figures 1–9.—Morphology of *Centruroides thorelli* Kraepelin 1891. 1–6, Lectotype male. 1, Left lateral aspect of metasomal segments III–V and telson; 2, Telson, enlarged view of left lateral aspect; 3, Telson, ventral aspect; 4, Dorsal aspect of pedipalp femur; 5, Dorsal aspect of pedipalp patella; 6, External (lateral) aspect of pedipalp chela. 7–9, Paralectotype female. 7, Left lateral aspect of metasomal segments III–V and telson; 8, Telson, enlarged view of left lateral aspect; 9, Ventral aspect of sternum, genital opercula, and pectines.

described mottled forms exist in southern Mexico and Central America. Two of these are described below and compared to the true *C. thorelli*.

Description of lectotype male.—*Coloration:* Base color yellow to light yellow brown. Cara-

pace with anterior margin infuscate and distinct dusky marbling throughout. Tergites with dusky band along posterior margins; anterior portions of tergites with diffuse dusky markings; each tergite bearing a narrow yellow median longitudinal line. Metasomal segments I–IV light yellow; V

and telson slightly darker. Cheliceral manus with dusky marbling. Pedipalps and legs pale yellow, with faint to moderate dusky markings. Venter uniformly yellowish. *Prosoma:* Carapace moderately coarsely granular; anterior median furrow deep, rounded; posterior median furrow deep, narrow near ocular tubercle and broadening posteriorly; carapacial carinae inconspicuous, indicated by medium-sized rounded granules. *Mesosoma:* Median carina on tergites I–II moderate, granular; on III–VI stronger, granular to crenulate. Pretergites minutely granular; post-tergites with large, smooth patches anterolaterally; posterior third of each tergite moderately coarsely granular. Tergite VII with strong, granular median keel and two pairs of strong, irregularly crenulate lateral keels. *Pectines:* Basal piece about 2.4 times wider than long with straight posterior margin; pectinal tooth count 16–16. Sternites III–VI smooth; VII with submedian and lateral carinae moderate, crenulate. *Metasoma:* (Fig. 1). Segments I–IV: Dorsolateral carinae on I strong, serratocrenulate; on II–III moderate, crenulate; on IV strong, crenulate. Lateral supramedian carinae on I strong, serratocrenulate; on II–IV strong, crenulate. Lateral inframedian carinae on I strong, serratocrenulate; on II–IV absent. Ventrolateral carinae on I moderate, granular to irregularly crenulate; on II–IV strong, crenulate. Ventral submedian carinae on I weak to moderate, granular; on II–IV strong, irregularly crenulate. Segment V: Dorsolateral carina moderate and crenulate anteriorly, weak and granular posteriorly; lateromedian carina essentially obsolete; ventrolateral and ventromedian carinae moderate, feebly crenulate. Intercarinal spaces on all segments sparsely granular. *Telson:* (Figs. 2, 3). Vesicle distinctly bilobed ventrodistally; aculeus downwardly deflected at junction with vesicle. Subaculear tooth strong, spinoid; its point directed towards tip of aculeus. Ventral aspect of vesicle irregularly granular. *Pedipalps:* Orthobothriotaxia A (Vachon 1974); femur with alpha-configuration of dorsal trichobothria (Vachon 1975). Femur: (Fig. 4). Dorsointernal and dorsoexternal carinae strong, serratocrenulate; ventrointernal carina strong, serrate; ventroexternal carina moderate, granular anteriorly and strong, serrate posteriorly; internal and external intercarinal spaces with large coarse granules. Patella: (Fig. 5). Dorsointernal carina moderate, finely serratocrenulate; dorsomedian and dorsoexternal carinae weak, granular; external carina weak, more or less smooth; ventroexternal carina weak, smooth; ventrointernal carina moderate, irregularly serratocrenulate; internal face with weak basal tubercle and several large granules. Chela: (Fig. 6). Dorsomarginal, digital, and ventroexternal carinae weak, smooth; dorsointernal carina obsolete except for a few coarse distal granules; other carinae essentially obsolete. Fixed finger with eight oblique rows of granules (the two basal rows are virtually fused, separated only by a tiny gap), flanked by supernumerary granules. Fixed finger trichobothrium *db* positioned just proximal to *et*. Movable finger with short apical row of four granules followed by seven rows of oblique granules (actually eight rows with two basal rows fused); granular rows flanked by supernumerary granules.

Morphometrics: See Table 1.

Measurements of lectotype male: (in mm; L = length, W = width, D = depth). Total L, 36.80; carapace L, 3.55; mesosoma L, 8.90; metasoma L, 20.95; telson L, 3.40. Metasomal segments: I L/W, 3.10/1.65; II L/W, 3.85/1.60; III L/W, 4.25/1.55; IV L/W, 4.70/1.55; V L/W, 5.05/1.50. Telson: vesicle L/W/D, 2.45/1.30/1.20; aculeus L, 0.95. Pedipalps: femur L/W, 3.90/0.85; patella L/W, 4.05/1.20; chela L/W/D, 6.20/1.25/1.30; fixed finger L, 3.35; movable finger L, 3.90; palm (underhand) L, 2.50.

Measurements of paralectotype female: Total L, 38.55; carapace L, 4.30; mesosoma L, 11.60; metasoma L, 18.85; telson L, 3.80. Metasomal segments: I L/W, 2.90/2.30; II L/W, 3.55/2.20; III L/W, 3.65/2.05; IV L/W, 4.15/2.10; V L/W, 4.60/2.05. Telson: vesicle L/W/D, 2.50/1.65/1.45; aculeus L, 1.30. Pedipalps: femur L/W, 4.10/1.20; patella L/W, 4.35/1.60; chela L/W/D, 7.15/1.45/1.65; fixed finger L, 4.00; movable finger L, 4.65; palm (underhand) L, 2.75.

Variation.—Female morphology differs from that of the male as follows: the metasomal segments are proportionately shorter (Fig. 7, Table 1), but the body excluding the metasoma is larger; the telson vesicle is more bulbous; pectinal tooth counts are slightly lower (see below); and the metasoma is more granular. The telson is more evenly ovoid and is not distally bilobed (Fig. 8). The basal piece of the female pectine is either straight or slightly convex (Fig. 9), similar to that of the male.

Male pectinal tooth counts varied as follows: 3 combs with 17 teeth, 4 combs with 16 teeth, and 9 combs with 15 teeth; female counts varied as follows: 4 combs with 15 teeth, 9 combs with 14 teeth, and 2 combs with 13 teeth (one comb

Table 1.—Morphometric comparisons between *Centruroides thorelli* Kraepelin, *C. schmidti* new species and *C. rileyi* new species. Ratios are as follows: 1 = carapace length/metasoma V length; 2 = pedipalp femur length/width; 3 = pedipalp patella length/width; 4 = metasoma III length/width; 5 = metasoma V length/width; 6 = metasoma V length/depth; 7 = pedipalp chela width/pedipalp patella width; 8 = pectinal basal piece width/length.

		Males			Females		
Ratio		*thorelli* (n = 7)	*schmidti* (n = 1)	*rileyi* (n = 1)	*thorelli* (n = 8)	*schmidti* (n = 1)	*rileyi* (n = 3)
1	min	0.612	0.651	0.833	0.920	0.809	0.872
	max	0.725			0.967		0.882
2	min	4.059	4.000	3.438	3.417	3.600	3.056
	max	5.158			3.857		3.444
3	min	3.000	2.818	2.652	2.719	2.645	2.345
	max	3.821			3.000		2.520
4	min	2.621	3.450	2.609	1.610	2.552	2.250
	max	3.471			1.780		2.375
5	min	3.241	4.300	3.429	2.190	3.241	2.833
	max	4.344			2.361		3.000
6	min	3.370	3.909	3.130	2.359	2.849	2.615
	max	4.633			2.528		2.786
7	min	0.917	0.818	0.783	0.893	0.774	0.759
	max	1.107			0.968		0.840
8	min	2.100	1.625	1.556	1.733	1.250	1.333
	max	2.625			2.364		1.429

was damaged and its teeth could not be counted). In addition, there were eight unsexed first instar specimens; among these juveniles, there were 2 combs with 16 teeth, 5 combs with 15 teeth, and 9 combs with 14 teeth.

Color varied somewhat among the specimens examined, with some individuals being lighter in base color with less intense fuscosity. The differences may be due to preservation, although *Centruroides* spp. are known to exhibit considerable variation in these characters.

Comments.—Hoffmann's (1932) specimens of *C. thorelli* from Tuxtla Gutiérrez, Chiapas and Francke & Stockwell's (1987) specimens from Costa Rica are not referable to *C. thorelli*. The latter authors noted significant differences between their specimens and the type series but opted not to describe their form as new. These specimens were not available for study. Although Armas (1992) reported only a small juvenile from Quintana Roo, I have been able to examine a mature female collected recently; as Armas has suggested (pers. comm.), it does not appear to be referable to *C. thorelli*.

Additional specimens examined.—GUATEMALA: Chichivac, near Tecpan (P. J. W. Schimdt, Leon Mandel Guatemala Expedition), 1 Feb 1934, 1♂, 1♀, 8 first instars (FMNH); Finca San Rafael, Sacatepequez, elev. 6900 ft., under bark (R. D. Mitchell), 24 June 1948, 1♂ (FMNH), 25 June 1948, 1♂, 1♀, 1 juv male (WDS), 29 June 1948, 2♂, 2♀ (FMNH).

Centruroides schmidti new species
(Figs. 10–18)

Type data.—Adult holotype male "found on bones of crocodile skull" at Lake Tickamaya, Honduras on 26 April 1923 by K. Schmidt and L. Walters (Capt. Field Mus. Exped.); permanently deposited in the Field Museum of Natural History, Chicago.

Etymology.—The specific epithet is a patronym honoring Dr. K. P. Schmidt, collector of the type specimens, for his many years of service to arthropod systematics at the Field Museum of Natural History.

Distribution.—Known only from Honduras and eastern Guatemala.

Comparative diagnosis.—*Centruroides schmidti* is similar to *C. thorelli*, but differs in the following characters: the mottling of the carapace, tergites, and legs is weaker; the distal segments of the metasoma and telson are much darker than the preceding segments; the male telson is not distally bilobed as in *C. thorelli*; the male sub-
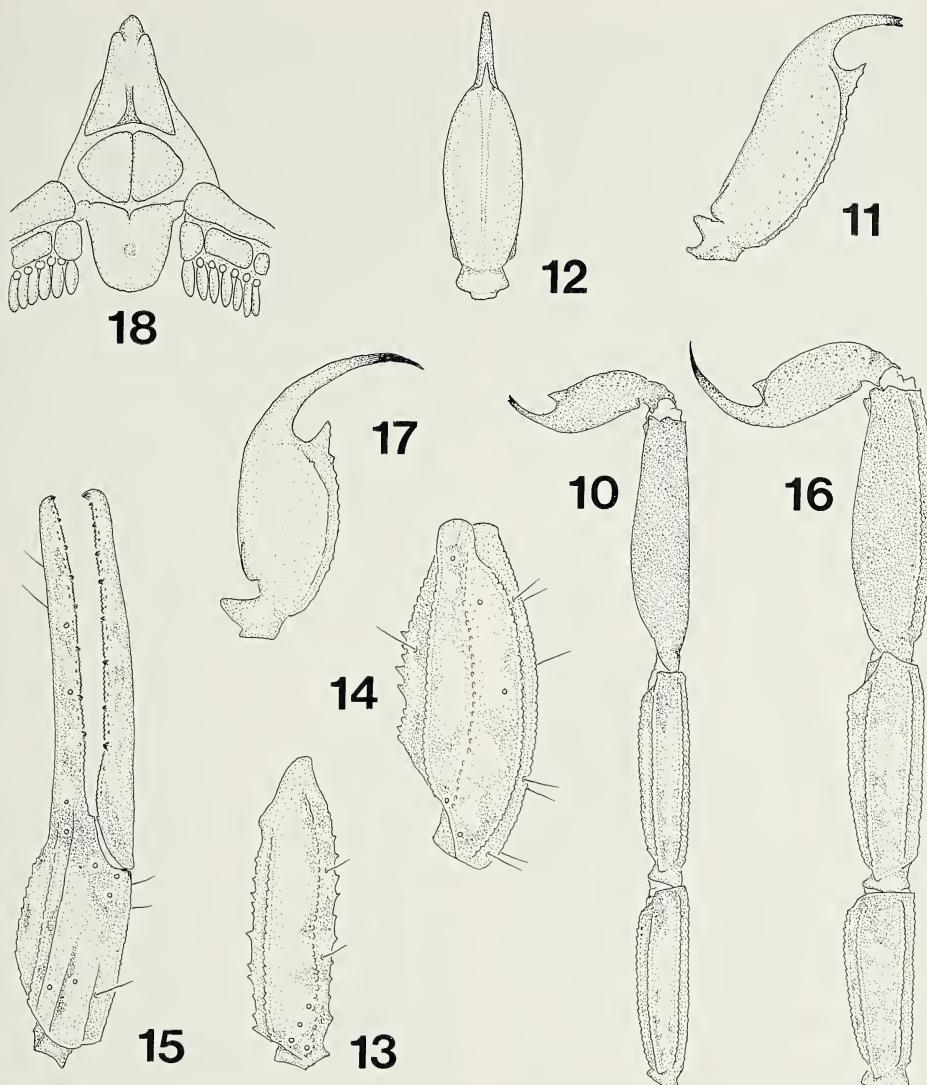
Figures 10–18.—Morphology of **Centruroides schmidti** new species. 10–15, Holotype male. 10, Left lateral aspect of metasomal segments III–V and telson; 11, Telson, enlarged view of left lateral aspect; 12, Telson, ventral aspect; 13, dorsal aspect of pedipalp femur; 14, Dorsal aspect of pedipalp patella; 15, External (lateral) aspect of pedipalp chela. 16–18, Paratype female. 16, Left lateral aspect of metasomal segments III–V and telson; 17, Telson, enlarged view of left lateral aspect; 18, Ventral aspect of sternum, genital opercula, and pectines.

aculear tubercle arises from a crenulated midventral carina and is angular, rather than a single spinoid tooth; metasomal segment V in the male is essentially acarinate, rather with the keels well developed; chela fixed finger trichobothrium *db* is slightly distal to *et* (rather than proximal to it); the basal piece of the female pectines is produced distally into a rounded lobe, rather than being straight or slightly convex; and there are several distinct morphometric differences (see Table 1).

Description of holotype male.—*Coloration:* Base color light yellow brown above with faint to moderate dusky markings on dorsum, chelicerae, pedipalps, legs, and sternites. Coloration fairly uniform except as follows: coxosternal region light yellow, pectines very pale yellow, metasomal segment V and telson dark orange to reddish brown; cheliceral teeth and tip of aculeus dark reddish brown. *Prosoma:* Carapace moderately coarsely granular; anterior median furrow moderately deep; posterior median furrow shal-

low anteriorly, deeper posteriorly; carapacial carinae inconspicuous, indicated by lines of small granules. *Mesosoma:* Median carina on I–VI moderate, granular. Pretergites minutely granular, post-tergites moderately, coarsely granular throughout. Tergite VII with moderate, granular median keel and two pairs moderate, finely serrated lateral keels. Pectinal basal piece 1.8 times wider than long; posterior margin distinctly rounded; pectinal tooth count 15–15. Sternites III–VI essentially smooth, with some fine granulation on VI; VII with submedian and lateral carinae moderate, finely serrate. *Metasoma:* (Fig. 10). Segments I–IV: Dorsolateral carinae on I–II moderate, finely serrate; on III moderate, crenulate; on IV weak, smooth. Lateral supramedian carinae on I–III moderate, finely serrate; on IV weak, smooth. Lateral inframedian carina on I moderate, serrate; on II–IV absent. Ventrolateral carinae on I–III moderate, finely serrate; on IV moderate, feebly granular. Ventral submedian carinae on I–III weak, finely serrate; on IV weak, feebly serrate. Intercarinal spaces shagreened. Segment V: Acarinate, intercarinal spaces shagreened. *Telson:* (Figs. 11, 12). Vesicle elongate oval in shape with gently rounded dorsal margin; ventral aspect with row of small granules leading to subaculear tubercle; subaculear tubercle narrow, but angular in lateral view, its point directed towards middle of aculeus. Ventral aspect of vesicle shagreened. *Pedipalps:* Orthobothriotaxia A (Vachon 1974); femur with alpha-configuration of dorsal trichobothria (Vachon 1975). Femur: (Fig. 13). Dorsointernal, dorsoexternal, and ventrointernal carinae strong, serrate; ventroexternal carina weak, smooth basally, crenulate distally; internal face with serrated keel flanked by accessory granules; dorsal face moderately granular. Patella: (Fig. 14). Ventrointernal carina strong, serrate; dorsointernal, dorsomedian, dorsoexternal, and ventroexternal carinae moderate, finely serrate; external carina moderate, feebly serrate. Inner face with seven larger, sharp, subconical granules. Chela: (Fig. 15). Dorsomarginal carina moderate, finely serrate; dorsal secondary carina moderate, granular to feebly crenulate; digital carina weak, smooth; external secondary carina weak, smooth; ventroexternal carina moderate, feebly granular; dorsointernal and ventrointernal carinae with relatively large, serrate granules. Fixed finger with eight oblique rows of granules, these flanked by supernumerary granules. Fixed finger trichobothrium *db* positioned just distal to *et*. Movable finger with short

row of four apical granules followed by eight oblique rows of granules; granular rows flanked by supernumerary granules.

Morphometrics.—See Table 1.

Measurements of holotype male.—(in mm, L = length, W = width, D = depth). Total L approximately 32 mm (tip of aculeus of telson broken, rendering total length an estimate); carapace L, 2.80; mesosoma L, 8.10; metasoma L, 17.20; telson L, ? *Metasomal segments:* I L/W, 2.50/1.15; II L/W, 3.05/1.05; III L/W, 3.45/1.00; IV L/W, 3.90/1.00; V L/W, 4.30/1.00. *Telson:* vesicle L/W/D, 1.75/080/0.85. *Pedipalps:* femur L/W, 2.80/0.70; patella L/W, 3.10/1.10; chela L/W/D, 4.70/0.90/0.95; fixed finger L, 2.85; movable finger L, 3.20; palm (underhand) L, 1.65.

Measurements of paratype female.—Total L, 37.35; carapace L, 3.80; mesosoma L, 11.20; metasoma L, 18.95; telson L, 3.40. *Metasomal segments:* I L/W, 2.90/1.55; II L/W, 3.45/1.45; III L/W, 3.70/1.45; IV L/W, 4.20/1.45; V L/W, 4.70/1.45. *Telson:* vesicle L/W/D, 1.90/1.10/1.25; aculeus L, 1.50. *Pedipalps:* femur L/W, 3.60/1.00; patella L/W, 4.10/1.55; chela L/W/D, 6.30/1.20/1.35; fixed finger L, 3.90; movable finger L, 4.50; palm (underhand) L, 2.10.

Variation.—Only the holotype male and paratype female were available for study. The female differs from the male in the following characters: the metasomal segments are not as elongate (Fig. 16), and metasoma V bears well developed crenulated ventrolateral and ventromedian carinae; the telson is slightly more globose (Fig. 17); and the basal piece of the pectines is produced distally into a large, rounded lobe (Fig. 18). Pectinal tooth counts in the male and female were similar: the male count was 15–15 and the female count 15–14.

Paratypes.—GUATEMALA: *Escobas,* Izabal, 27 November 1933 (K. P. & P. J. W. Schmidt, Leon Mandel Guatemala Exped.), 1♀ (FMNH).

Centruroides rileyi new species
Figs. 19–27

Type data.—Adult holotype male and adult paratype female from Bocatoma (= 7 km SSE Gomez Farias), Tamaulipas, Mexico on 25–30 March 1978 by E. G. Riley; permanently deposited in the collection of the United States National Museum (Smithsonian), Washington, D. C.

Etymology.—The specific name is a patronym honoring Dr. Edward Riley of Texas A & M University, the collector of the holotype.
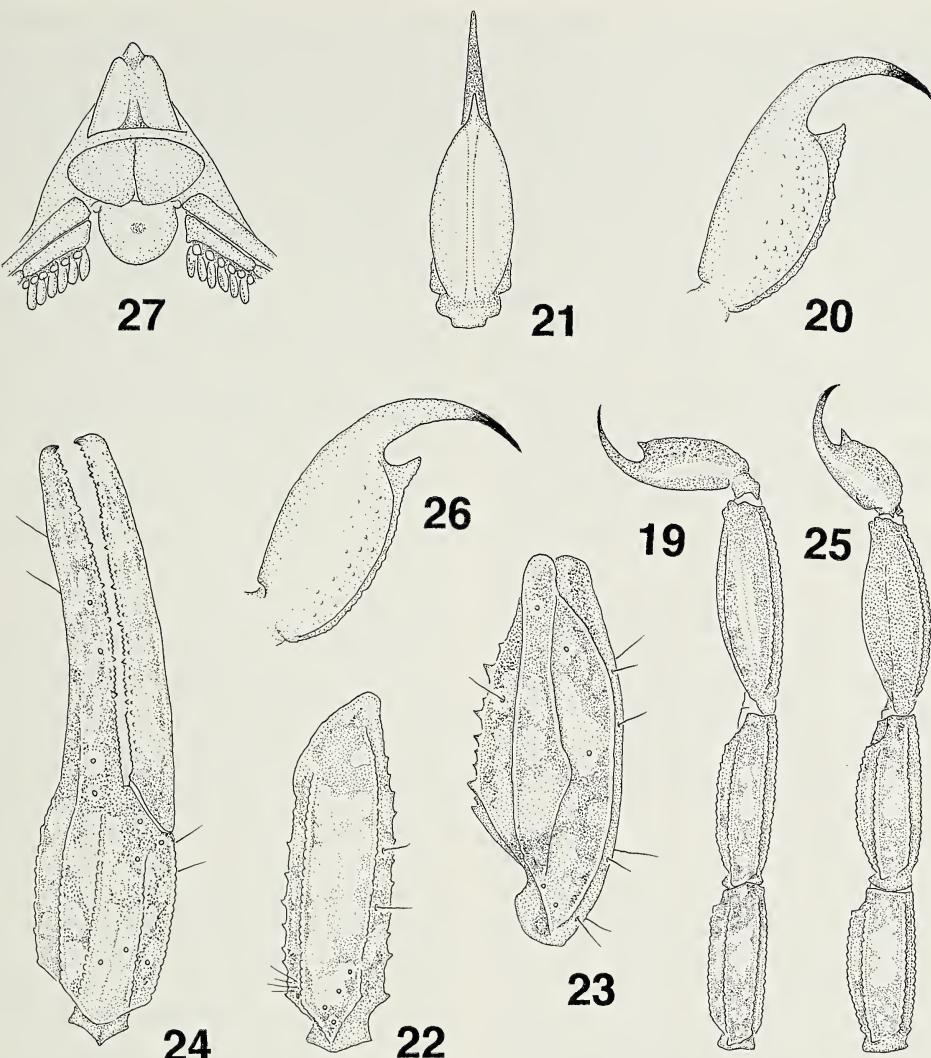
Figures 19–27.—Morphology of **Centruroides rileyi** new species. 19–24, Holotype male. 19, Left lateral aspect of metasomal segments III–V and telson; 20, Telson, enlarged view of left lateral aspect; 21, Telson, ventral aspect; 22, Dorsal aspect of pedipalp femur; 23, Dorsal aspect of pedipalp patella; 24, External (lateral) aspect of pedipalp chela. 25–25, Paratype female. 25, Left lateral aspect of metasomal segments III–V and telson; 26, Telson, enlarged view of left lateral aspect; 27, Ventral aspect of sternum, genital opercula, and pectines.

Distribution.—Known from several localities in southern Tamaulipas and northern San Luis Potosi, Mexico.

Comparative diagnosis.—*Centruroides rileyi* is most similar to *C. schmidti*, but is clearly related to *C. thorelli* as well. Unlike the other two species, sexual dimorphism in the length of the metasomal segments is not as pronounced; male segments are more slender but not noticeably longer than those of the female. Based on the material at hand, *C. rileyi* exhibits smaller body

size than either *C. thorelli* or *C. schmidti*. The shape of the subaculear tubercle is similar to that of *C. schmidti*, developed from a distinct ventromedian keel. Likewise the basal piece of the female pectines is produced distally into a rounded lobe, a feature seen in *C. schmidti* but not in *C. thorelli*. Among specimens available, female pectinal tooth counts were slightly lower than in *C. schmidti*, with a range of 11–13 (13–15 in *C. thorelli* and 14–15 in *C. schmidti*). Metasomal segment V in the male of *C. rileyi* bears distinct

(but weak) crenulate carinae; these carinae are developed in *C. thorelli*, but not in *C. schmidti*. The dorsal carinae of the pedipalp chelae are moderately to strongly developed and distinctly crenulate, but are feeble and smooth to granular in *C. thorelli* and only the dorsal marginal carina is noticeably crenulated in *C. schmidti*. Morphometric comparisons are provided in Table 1.

Description of holotype male.—*Coloration:* Base color yellow to light yellow brown. Carapace with distinct dusky marbling concentrated mostly in median area. Tergites with distinct, regular pattern of blackish spots. Metasomal segments I–IV light yellow, moderately infuscate; V and telson more heavily infuscate, appearing darker than preceding segments. Cheliceral manus with strong dusky marbling. Pedipalps and legs yellow, with distinct dusky markings. Venter uniformly yellowish anteriorly; sternites lightly infuscate. *Prosoma:* Carapace moderately coarsely granular; anterior median furrow moderately deep; posterior median furrow shallow anteriorly, deeper posteriorly; carapacial carinae weak, indicated by lines of small granules. *Mesosoma:* Median carina on tergites I–IV moderate, granular; on V–VI moderate, granular to crenulate. Pretergites minutely granular, posttergites with large, smooth patches anterolaterally; posterior third of each tergite moderately, coarsely granular. Tergite VII with moderate, granular median keel and two pairs strong, finely serrated lateral keels. Pectinal basal piece 1.6 times wider than long; posterior margin distinctly rounded; pectinal tooth count 14–14. Sternites III–VI essentially smooth; VII with submedian carinae weak, granular and lateral carinae moderate, finely serrate. *Metasoma:* (Fig. 19). Segments I–IV: Dorsolateral carinae on I–II strong, finely serrate; on III strong, irregularly crenulate; on IV moderate, crenulate. Lateral supramedian carinae on I–III strong, finely serrate; on IV strong, feebly serrate. Lateral inframedian carina on I strong, finely serrate; on II–IV absent. Ventrolateral carinae on I–III strong, finely serrate; on IV strong, feebly serrate. Ventral submedian carinae moderate, feebly serrate; on IV weak, feebly serrate. Segment V: Dorsolateral carina moderate, feebly granular; lateromedian carina obsolete; ventrolateral and ventromedian carinae moderate, feebly serrate. All metasomal intercarinal spaces sparsely granular. *Telson:* (Fig. 20–21). Vesicle elongate oval in shape with aculeus moderately deflected downward; ventral aspect with median longitudinal row of small granules

leading to subacular tubercle; subacular tubercle narrow, but angular in lateral view, its point directed towards middle of aculeus. Ventral aspect of vesicle lightly granular. *Pedipalps:* Orthobothriotaxia A (Vachon 1974); femur with alpha-configuration of dorsal trichobothria (Vachon 1975). Femur: (Fig. 22). All carinae strong, serrate; internal face with series of large serrate granules; dorsal face moderately granular. Patella: (Fig. 23). Dorsointernal carina moderate, serrate; dorsomedian and dorsoexternal carinae strong, serratocrenulate; external carina strong, feebly crenulate; ventroexternal carina moderate, crenulate; ventrointernal carina moderate, irregularly serrate. Inner face with eight to ten larger, sharp, subconical granules. Chela: (Fig. 24). Dorsomarginal carina strong, coarsely crenulate; dorsal secondary carina strong, finely serrate; digital and external secondary carinae moderate, finely crenulate; ventroexternal carina strong, finely crenulate; ventrointernal carina moderate with a few rounded granules; dorsointernal carina strong, coarsely serrate. Fixed finger with eight oblique rows of granules flanked by supernumerary granules. Fixed finger trichobothrium *db* positioned just distal to *et*. Movable finger with short apical row of four granules followed by eight oblique rows of granules; granular rows flanked by supernumerary granules.

Morphometrics.—See Table 1.

Measurements of holotype male.—(in mm; L = length, W = width, D = depth). Total L, 29.75; carapace L, 3.00; mesosoma L, 9.10; metasoma L, 15.15; telson L, 2.50. *Metasomal segments:* I L/W, 2.35/1.30; II L/W, 2.80/1.20; III L/W, 3.00/1.15; IV L/W, 3.40/1.05; V L/W, 3.60/1.05. *Telson:* vesicle L/W/D, 1.50/0.80/0.90; aculeus L, 1.00. *Pedipalps:* femur L/W, 2.75/0.80; patella L/W, 3.05/1.15; chela L/W/D, 4.75/0.90/1.05; fixed finger L, 2.85; movable finger L, 3.25; palm (underhand) L, 1.65.

Measurements of female paratype.—Total L, 29.85; carapace L, 3.15; mesosoma L, 9.40; metasoma L, 14.65; telson L, 2.65. *Metasomal segments:* I L/W, 2.25/1.40; II L/W, 2.65/1.25; III L/W, 2.85/1.20; IV L/W, 3.30/1.20; V L/W, 3.60/1.20. *Telson:* vesicle L/W/D, 1.45/0.85/0.95; aculeus L, 1.20. *Pedipalps:* femur L/W, 2.75/0.85; patella L/W, 3.15/1.25; chela L/W/D, 4.90/1.05/1.10; fixed finger L, 3.00; movable finger L, 3.45; palm (underhand) L, 1.60.

Variation.—Only a single adult male is known; however, there are three adult female specimens and a juvenile. Females differ from the males

only slightly in metasomal morphometrics with the male metasoma being scarcely longer, but noticeably thinner (Fig. 25). There is also little difference in the shape of the telson (Fig. 26). Finally, the female pectinal basal piece is produced distally into a distinct, rounded lobe (Fig. 27). Female pectinal tooth counts were as follows: there were one comb with 11 teeth, four combs with 12 teeth, and one combs with 13 teeth.

Paratypes.—MEXICO: *San Luis Potosi*, 5 km N Tamazunchale off Hwy 85, 1 August 1987 (J. A. Nilsson), 1♀ (JAN). *Tamaulipas*, Gomez Farias, 16 March 1977 (R. Schmidt), 1♀ (FSCA).

ACKNOWLEDGMENTS

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DISTRIBUTIONS OF THE SCORPIONS *CENTRUROIDES VITTATUS* (SAY) AND *CENTRUROIDES HENTZI* (BANKS) IN THE UNITED STATES AND MEXICO (SCORPIONES, BUTHIDAE)

Rowland M. Shelley: North Carolina State Museum of Natural Sciences, P. O. Box 29555, Raleigh, North Carolina 27626-0555 USA

W. David Sissom: Department of Biology & Geosciences, West Texas A & M University, P. O. Box 808, Canyon, Texas 79016-0001 USA

ABSTRACT. Specific locality records are presented to define the distributions of the scorpions *Centruroides vittatus* (Say) and *C. hentzi* (Banks) in North America. The former occurs in the Central Plains as far north as Thayer County, Nebraska; the Rio Grande and Sangre de Cristo Mountains form the western distributional boundary, and the Missouri and Mississippi Rivers essentially do likewise on the east. *Centruroides vittatus* occurs just across the latter watercourses in Holt County, Missouri, and Monroe and Randolph counties, Illinois, range extensions that probably can be attributed to rafting or natural alterations in the rivers' courses. Other occurrences east of the Mississippi River, in northern Illinois, Kentucky, Tennessee, Louisiana, Mississippi and North Carolina, are associated with cities and are mostly far outside what we consider the natural range; such records are regarded as human introductions. One of these apparently represents a viable reproducing population in Rutherford County, Tennessee. Likewise, records far west of the Rio Grande, in Arizona and California, are interpreted as introductions. *Centruroides vittatus* traverses the Rio Grande south of Texas and occurs in Chihuahua, Coahuila, Nuevo Leon, and Tamaulipas, Mexico. *Centruroides hentzi*, previously known only from Florida in the United States, occurs in Mobile and Baldwin counties, Alabama, and in the southern tier of counties in Georgia. Occurrences of *C. hentzi* in Durham, Carteret, and Brunswick counties, North Carolina, Charleston County, South Carolina, and Harris and Muscogee counties, Georgia, are considered to represent accidental human importations, although it is also possible that the more proximal ones are peripheral isolates.

The scorpion fauna of the United States east of the Mississippi River is depauperate in comparison to that of the southwest. According to Muma (1967), five species – *Tityus floridanus* Banks, *Isometrus maculatus* (DeGeer), *Centruroides gracilis* (Latreille), *C. hentzi* (Banks), and *C. keysi* Muma – occur in Florida. Presently, *T. floridanus* is a synonym of *T. dasyurus* Pocock, from Puerto Rico and the Virgin Islands (Lourenço & Francke 1984), and *C. keysi* is considered a synonym of *C. guanensis* Frangillo, from Cuba, Hispaniola, and the Bahamas (de Armas 1981). The first two species are known in Florida only from single individuals ostensibly collected at Key West. These records are questionable, and *C. gracilis*, *hentzi* and *guanensis* are the only scorpions that will be encountered frequently in the state, if not the only ones actually occurring there. Elsewhere in the East, the only known native scorpion is *Vaejovis carolinianus* (Beauvois), an upland species occurring primarily north and west of the Fall Zone as far north as the Ohio River in central Kentucky (Shelley 1994a).

Say (1821) described "*Buthus vittatus*" from the "sea islands" of Georgia, but his type specimen(s) are lost, and this name, long associated with the common midwestern species of *Centruroides*, was formally assigned to it (Opinion 1680, 1992) in response to the petition by Stockwell & Levi (1989), as subsequently modified by respondent comments (Gentry et al. 1991). As part of this opinion, a neotype of *B. vittatus* was designated from Kinney County, Texas, instead of Georgia. Say's locality record plausibly refers to *C. hentzi*, which occurs statewide in Florida (Muma 1967), but up to now is not supported by preserved specimens. *Centruroides hentzi* and *vittatus* have been introduced into North Carolina (Shelley 1994b), and newspaper articles have reported scorpions from Kiawah Island and Isle of Palms, near Charleston, South Carolina (Langley 1991, 1994). These two scorpions are
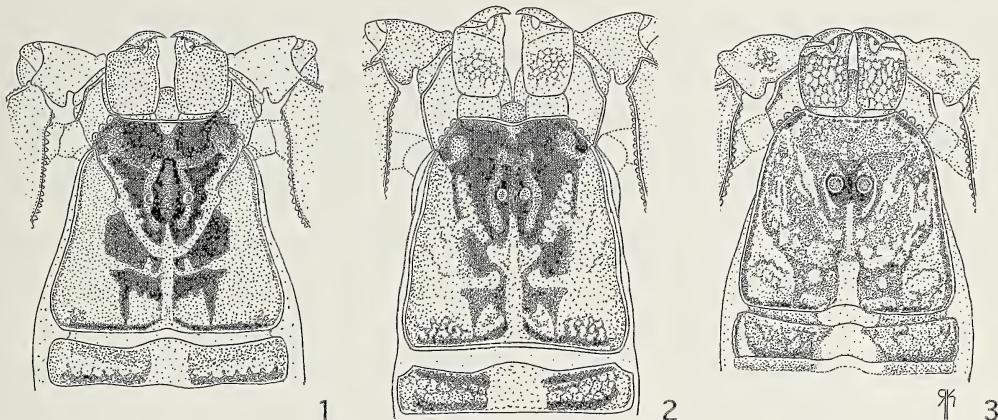
Figures 1–3.—Comparisons between *Centruroides vittatus* and *C. hentzi* in color patttern. 1, 2, Dorsal views of carapace and chelicerae of *C. vittatus*; 3, Same for *C. hentzi*.

readily distinguished at any life stage by the characters in Table 1, which also serve to distinguish *C. vittatus* from *C. guanensis* (= *C. keysi*). Differences in the pigmentations of the chelicerae and carapaces, and in the configurations of the telsons, are shown in Figs. 1–5.

While recently examining museum specimens, we encountered samples of *C. hentzi* from southern Alabama and Georgia, thus establishing its occurrence north and west of Florida. The museum holdings also included numerous new records of *C. vittatus* that enable a detailed description of its distribution. This distribution has been generally described as Louisiana west of the Mississippi River to New Mexico east of the Rio Grande, and from the Central Plains of the United States to northern Mexico (Stahnke & Calos 1977; Stockwell & Levi 1989; Shelley 1994b). However, it is striking to note that, aside from Las Vegas, San Miguel County, New Mexico (Banks 1901); Cleveland, Garvin, and Seminole counties, Oklahoma (cited as *Centrurus carolinianus* by Banks et al. 1932); the Wichita Mountains, Comanche County, Oklahoma (Cokendolpher & Bryce 1980); and Thayer County, Nebraska (Rapp 1987), few definite United States records exist outside of Texas, where *C. vittatus* can be anticipated statewide with perhaps the exception of several southeastern coastal counties. Published Mexican records (Hoffmann 1932; Diaz Najera 1975) are as follows: Cd. Juarez in Chihuahua; Cd. Acuna, Allende, Cuatro Cienegas, Lamadrid, and Sacramento in Coahuila; Hidalgo in Nuevo Leon; and Barrotal, Cd. Aleman,

Guerrero, Matamoros, and San Fernando in Tamaulipas.

It is our purpose here to place the new samples on record, update the known distributions of these scorpions in the United States and Mexico, and provide additional habitat information based on notations on vial labels. Acronyms for sources of preserved material are as follows: AMNH - American Museum of Natural History, New York, New York; ANSP - Academy of Natural Sciences, Philadelphia, Pennsylvania; CAS - California Academy of Sciences, San Francisco; CC - Biology Department, Columbus College, Columbus, Georgia; CIM - Cumberland Island Museum, St. Marys, Georgia; FMNH - Field Museum of Natural History, Chicago, Illinois; FSCA - Florida State Collection of Arthropods, Gainesville; INHS - Illinois Natural History Survey, Champaign; LSU - Entomology Department, Louisiana State University, Baton Rouge; MCZ - Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MEM - Mississippi Entomological Museum, Mississippi State University, Starkville; MMNS - Mississippi Museum of Natural Science, Jackson; MPM - Milwaukee Public Museum, Milwaukee, Wisconsin; MWSU - Midwestern State Univ., Wichita Falls, TX; NCSM - North Carolina State Museum of Natural Sciences, Raleigh; NCSU - Entomology Department, North Carolina State University, Raleigh; NMNH - National Museum of Natural History, Smithsonian Institution, Washington, DC; OKSU - Emerson Entomological Museum, Oklahoma State University, Still-
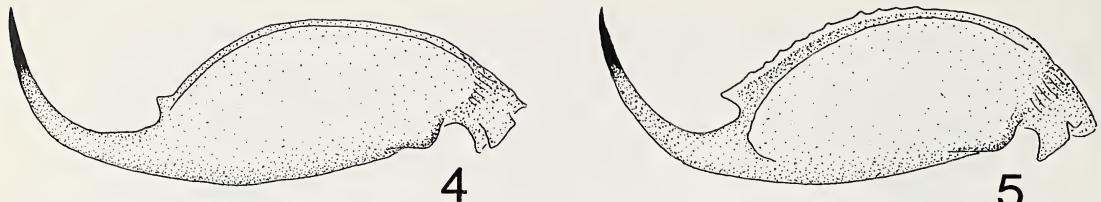
Figures 4–5.—Differences in telson morphology between *Centruroides vittatus* and *C. hentzi*. 4, Lateral view of telson of *C. vittatus*; 5, Same for *C. hentzi*.

water; OMNH - Oklahoma Museum of Natural History, University of Oklahoma, Norman; PMNH - Peabody Museum of Natural History, Yale University, New Haven, Connecticut; RNH - Private collection of R. N. Henson, Boone, North Carolina; SEM - Snow Entomological Museum, University of Kansas, Lawrence; SFASU - Biology Department, Stephen F. Austin University, Nacogdoches, Texas; TAMU - Texas A & M University, College Station; TMM - Texas Memorial Museum, University of Texas at Austin; TY - private collection of T. Yamashita; UCO - University of Colorado Museum, Boulder; UGA - University of Georgia Museum of Natural Histor, Athens; UMN - Entomology Department, University of Minnesota, St. Paul; UMO - Enns Entomological Museum, University of Missouri, Columbia; UTEP - Biology Department, University of Texas at El Paso; WDS - Private collection of W. D. Sissom, Canyon, Texas; WFR - Private collection of W. F. Rapp, Crete, Nebraska; WTAMU - Department of Biology and Geosciences, West Texas A&M University, Canyon, Texas.

Centruroides vittatus
Figs. 1, 2, 4, 6, 7

Habitat.—As reported by Shelley (1994b) and recorded through personal observations, *C. vittatus* occupies a variety of microhabitats in deserts, deciduous and pine forests, and grasslands, inhabiting crevices of rocky outcrops, canyon walls, and volcanic hills, climbing into vegetation, seeking refuge beneath yuccas and in trash dumps, and commonly entering houses. It has been collected from sea level to elevations of over 1800 m in the Guadalupe and Chisos Mountains, Texas and 2340 m in mountains of Coahuila, Mexico. Additional microhabitats cited on labels with the present samples include under palm branches, rocks, bark and logs in a pine forest, cow dung, and old rags and debris at an aban-

doned campsite; in a sabal palmetto grove; in the nest of a cactus rat; and in a molasses trap left overnight. Specimens were found in homes, motels, dormitories, and office buildings in Cole, St. Louis, and Taney counties, Missouri; Orleans Parish, Louisiana; Alfalfa, Kay, Marshall, Muskogee, Pawnee, Payne, and Stephens counties, Oklahoma; and DeBaca and Eddy counties, New Mexico. An individual from San Miguel County, New Mexico, was encountered inside the Las Vegas hospital.

Distribution.—*Centruroides vittatus* has officially been recorded from only 16 Texas counties – Andrews, Brewster, DeWitt, Edwards, Erath, Garza, Hall, Kinney, Lubbock, Mason, Parker, Travis, Uvalde, Val Verde, Williamson, and Wise (Reddell 1965, 1970; Rowland & Reddell 1976; Stockwell & Levi 1989; Formanowicz & Shaffer 1993). Although overlooking a number of significant collections, Stockwell (1986) reported it from 50 additional counties in an unpublished Master's Thesis: Archer, Bexar, Blanco, Cameron, Clay, Coke, Crockett, Crosby, Culberson, Dallas, Foard, Gillespie, Gonzales, Grayson, Hidalgo, Jeff Davis, Johnson, Kaufman, Kent, Kerr, Kimble, King, Knox, LaSalle, Maverick, McMullen, Medina, Menard, Motley, Navarro, Oldham, Pecos, Presidio, Real, Reeves, San Patricio, San Saba, Schleicher, Starr, Sutton, Taylor, Terrell, Tom Green, Victoria, Ward, Webb, Wichita, Winkler, Zapata, and Zavala. These records are scattered across the state, and the scorpion is now known from bordering states in the United States and Mexico in all directions. We therefore believe that *C. vittatus* can be anticipated in every Texas county except perhaps Orange, Jefferson and Chambers, along the Gulf Coast east of Galveston Bay. Present records from Louisiana do not support its occurrence in this corner of Texas, and field collecting is needed in these counties and in Calcasieu and Cameron Parishes, Louisiana, to confirm or refute this
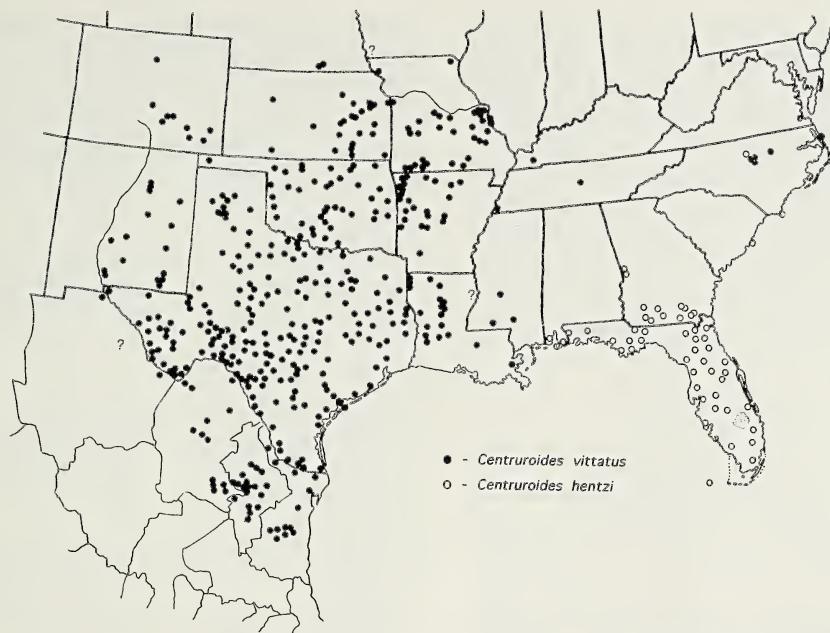
Figure 6.—Distributions of *C. vittatus* (closed circles) and *C. hentzi* (open circles) in the United States and Mexico. Florida records for *C. hentzi* are for counties only and are partially based on Muma (1967). The approximate courses of the Missouri River and the Rio Grande are indicated in Missouri and New Mexico/Colorado, respectively. The "?" in Iowa and Louisiana denotes the records from unknown counties along the Missouri and Mississippi Rivers, respectively. The "?" in Chihuahua, Mexico reflects our lack of knowledge on the extent of the distribution of *C. vittatus* in this region, which has been so poorly sampled.

finding. Large numbers of samples from Texas exist in many museum collections, too many to be shipped for examination. We therefore list only additional Texas county records that were intermingled with material from other states, but plot all known localities accurately on Fig. 6.

Determining the natural distribution of *C. vittatus*, and to a lesser extent *C. hentzi*, is hampered by the number of specimens that man has accidentally transported into new areas, which tend to mask the indigenous range. Samples from distant states like California and North Carolina clearly represent human introductions, but ones from proximate sites like Memphis, Tennessee and Baton Rouge, Louisiana could plausibly reflect peripheral native populations. Mapping of all the samples, however, reveals clusters of records that we believe represent natural occurrence; we use them as the basis for determining indigenous distributions, particularly when detached records are from urban environments and are consistent with human activities. Thus, as shown in Fig. 7, the eastern border formed by clustered records angles southwestward through southeastern Missouri into Arkansas, and then

runs through central Arkansas and Louisiana before turning westward into Texas, omitting the adjoining coastal corners of Louisiana and Texas. The only outlying records along this boundary are from the urban environments of Baton Rouge and Memphis, and are therefore treated as human introductions.

The overall distribution of *C. vittatus* (Fig. 6) extends southward from Thayer County, Nebraska, and expands longitudinally to encompass all of Oklahoma, Arkansas, and Missouri south of the Missouri River. The Rio Grande in southern New Mexico and the Sangre de Cristo Mountains in northern New Mexico and south central Colorado form the western geographical boundary, and present Colorado records suggest westward expansion through the Arkansas River Valley. The only available records from the western half of Kansas are sight records from Clark and Trego counties, so collecting is needed to determine the distribution in this part of the state. The Missouri and Mississippi Rivers essentially form distributional boundaries, as the only natural occurrences to the north/east of the former, in Holt County, Missouri, and to the east of the

latter, in Monroe and Randolph counties, Illinois, are in bordering counties that could have resulted from rafting or natural alterations of the rivers' courses; the Illinois records are directly across the Mississippi from an area where the scorpion is common in Missouri. However, other sites east of the Mississippi, mostly urban areas, represent obvious adventives. The range traverses the Rio Grande south of Texas, and *C. vittatus* is known from over half the lengths of Tamaulipas, Nuevo Leon, and Coahuila, and the northern periphery of Chihuahua.

NEW RECORDS

Specimens that are considered to represent the native distribution were examined from the following localities. Missing data (exact locality, date of collection, and collector(s)) are not reported. Sight records deemed reliable from additional counties are presented separately for each state after the locality listings but are plotted in Fig. 6.

USA: **ARKANSAS:** *Benton County*, Pea Ridge Natl. Battlefield, 23 April 1965, J. D. Unzicker (INHS). *Boone County*, Harrison, Conard Fissure, 8 June 1932, F. D. Wood (PMNH). *Cleburne Co.*, 9.6 km SSW Drasco, September 1979, D. Pearson (MPM). *Crawford County*, 14.4 km N Mountainsburg, Boston Mts., 30 June 1955, T. J. Cohn (AMNH); and Lee Creek, 9 July 1968, R. & A. Graves (FSCA). *Faulkner County*, 12.8 km N Camp Robinson, 21 April 1943, D. D. Davis (FMNH); Camp Robinson, 24 March 1943, R. C. Ellis (FMNH). *Franklin County*, 6.4 km N Ozark, along AR hwy. 23, 12 October 1963 and 15 September 1964, Unzicker, Yamamoto, Rotramel (INHS). *Garland County*, 17.6 km W Hot Springs, 21 March 1958, K. P. Schmidt. *Izard County*, May 1954, H. M. Bevel (MCZ). *Logan County*, Mt. Magazine, 21 June 1938, J. M. Schmidt (FMNH), 13 August 1966 and 13 April 1976, L. D. Newsome (LSU), and 15 July 1949, M. W. Sanderson, Stannard (INHS); 1.6 km S Ione, along AR hwy. 23, 15 September 1964, J. D. Unzicker (INHS); and 16 km S Booneville, along AR hwy. 23, 12 October 1963, Unzicker, Yamamoto (INHS). *Marion County*, 6.4 km SW Oakland, Ozark Isle Park, Bull Shoals L., 28 July 1970, P. J. Clausen (FSCA). *Nevada County*, 30 December 1954, N. B. Causey (MCZ). *Newton County*, Buffalo National River, near Pruitt, no date, T. Yamashita (TY). *Perry County*, Williams Jct., Ouachita Mts., 19 July 1968, E. N. K. Waering (FSCA). *Pike County*, Kirby, 9 June 1970 (WTAMU); and Glenwood, 23 July 1973 (WTAMU). *Polk County*, Mena, 10 March 1956, N. B. Causey (MCZ). *Pulaski County*, North Little Rock, 26 April 1962, J. Ball (MCZ); Little Rock, summer 1943, E. M. Nelson (FMNH); Pinnacle Mt. State Park, no date, T. Yamashita (TY); Camp Robinson, 9 May 1944, L. Hook (AMNH); and 12.9

Table 1.—Morphological differences between *C. vittatus* and *C. hentzi* and *C. guanensis* (=*C. keysi*).

C. vittatus	*C. hentzi/C. guanensis*
1. Carapace with black inverted triangle covering ocular tubercle (Figs. 1–2)	Carapace uniformly light mottled brown (Fig. 3)
2. Dorsal surface of chelicerae usually uniformly yellowish (Fig. 1), occasionally with trace of reticulation (Fig. 2)	Dorsal surface of chelicerae with distinct brown reticulation (Fig. 3)
3. Pedipalp chela fingers and manus uniformly yellowish; all pedipalpal segments uniformly yellowish	Pedipalp chela fingers infuscate; pedipalpal segments with dusky marbling
4. Median yellow stripe of dorsum as wide or wider than black stripes (when stripes are present)	Median yellow stripe usually about half as wide as black stripes
5. Higher pectinal tooth counts Male: 21–30 Female: 20–27	Lower pectinal tooth counts Male: 17–19 Female: 16–18
6. Metasomal segments with a single solid dusky midventral stripe lying between ventral submedian carinae	Metasomal segments with entire ventral aspect of metasomal segments infuscate with pale spots marking positions of setae
7. Legs usually immaculate yellow, rarely faintly infuscate	Legs moderately to heavily infuscate
8. Telson suboval when viewed from ventral aspect	Telson broadest apically, with subtle "shoulders"
9. Telson midventrally with very weak smooth, longitudinal carina leading into subaculear tubercle (Fig. 4)	Telson ventrally with moderate, crenulate carina leading into subaculear tubercle (Fig. 5)
10. Subaculear tooth small, spinoid (Fig. 4)	Subaculear tooth larger, angular (Fig. 5)

km N Camp Robinson, 21 April 1943, D. D. Davis (FMNH). *Scott County*, nr. Boles, 9 September 1967, D. M. Smith (INHS). *Sharp County*, 0.4 km SW Ash Flat, 16 September 1964 (INHS). *Washington County*, 24 km W Prairie Grove, Cove Cr. Valley, Boston Mtns., February 1956, M. Hite (MCZ); Prairie Grove, 20 October 1955, M. Hite (MCZ); Fayetteville, no date, T.
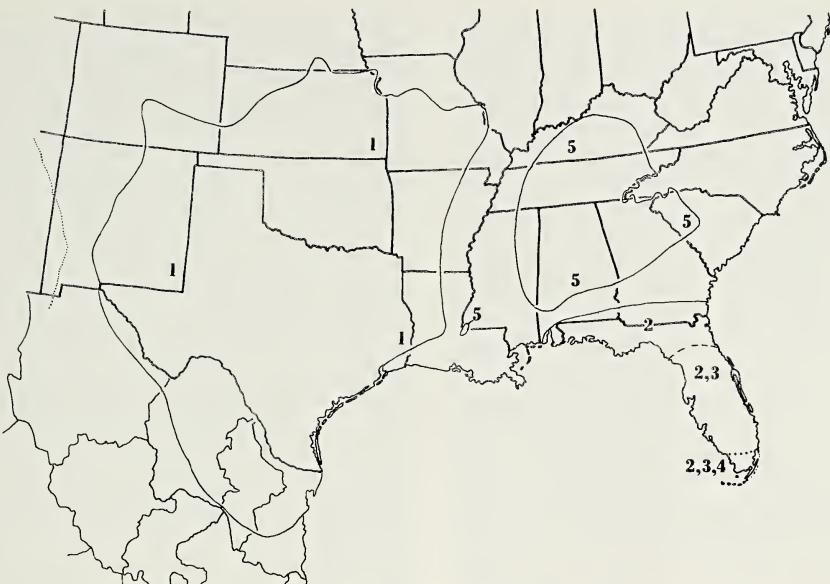
Figure 7.—Comparisons of native distributions of scorpions in the United States and northern Mexico, emphasizing those species occurring in eastern and southcentral United States. 1, *C. vittatus*; 2, *C. hentzi*; 3, *C. gracilis*; 4, *C. guanensis* (= *C. keysi*); 5, *Vaejovis carolinianus*. The dotted line in western New Mexico and Arizona indicates the eastern boundary of the range of *C. exilicauda* (Wood); the boundary in New Mexico is based on the unpublished data of the junior author.

Yamashita (TY); Fayetteville, 4 October 1938, L. G. Hembest (NMNH) and 19 July 1953, N. B. Causey (MCZ); and 40 km W Fayetteville, 20 July 1969, A. Graves (FSCA). Sight records (T. Yamashita, in litt. to second author): Lake Ouachita (several sites, all rocky areas) in Hot Springs Co. **COLORADO:** *Baca County*, Regnier, ca. 36.8 km S Pritchett, Comanchee Nat. Grassland (AMNH). *Fremont County*, 0.8 km W Canon City, 5 September 1958, A. W. Spencer (CAS); and Canon City, June 1968, R. L. Kaesler (SEM), and outside Fly Cv., 28 August 1961, W. J. Gertsch, W. Ivie (AMNH). *Las Animas County*, along CO hwy. 109, 21 June–11 July 1966 (AMNH). *Otero County*, along CO hwy. 109, 6 July 1967 (AMNH). *Prowers County*, Two Buttes Reservoir, 3–19 July 1966 (AMNH). *Pueblo County*, Boone, 6 July–1 August 1967 (AMNH); along CO hwy. 78, 16 March 1963–15 August 1964 (AMNH); and Lime, ca. 16 km S, 3.2 km E Pueblo, 12 May year unknown, Brookhart (AMNH). **ILLINOIS:** *Monroe County*, 6.4 km N Fults, 9 April 1949, D. M. Smith (INHS); 4 km N Fults, 13 July 1949, A. G. Wright (INHS); Fults, 9 October 1948 and 16 June 1949, P. W. Smith (CAS, INHS), 15 July 1953, Hensley & Smith (INHS), and spring 1971, D. Daleske (FMNH); and 6.4 km S Valmeyer, 1 May 1956, P. W. Smith (INHS). *Randolph County*, 3.2–4.8 km N Prairie du Rocher, October 1980, R. W. Sites (UMO); and Prairie du Rocher, 28 June 1949, Smith & Stannard (INHS) and 29 September 1982, J. H. Gerrard (AMNH). **KANSAS:** *Allen County*, Humboldt, 24 August 1944 (CAS).

Chase County, 2.4 and 4.8 km S Saffordville, 24 June 1964 and 10 May 1965, R. F. Clarke (CAS), and 11.2 km S Saffordville, 20 June 1965, R. Zwiefel (AMNH); 8 km S Strong City, 4 June 1957, C. E. Goulden (CAS); and east edge L. Kahola, 17 June 1965, R. F. Clarke (CAS). *Chautauqua County*, 4.8 km W Peru, 3 April 1933, C. E. Burt (NMNH). *Cowley County*, Winfield vic., 1933, C. E. Burt, B. Anderson (NMNH). *Douglas County*, Lawrence, B. C. Marshall (ANSP), 10 October 1947 (CAS), 28 April 1948 (INHS), and 22 September 1962 (SEM); Lawrence, no date, T. Yamashita (TY); prairie outside Lawrence, 3 May 1964, S. Roth (CAS); 4.8 km W Lawrence, Clinton Lake Rec. Area, 9 May 1993, B. Cutler (UMN); and Rock Cr., 3 May 1899 (NMNH). *Lyon County*, Emporia, 14 May and 21 September 1966 (CAS). *Osage County*, 17 April 1966, R. F. Clarke (CAS). *Reno County*, Hutchinson, 27 July 1951 (CAS). *Riley County,* Manhattan, 10–19 September 1904 (MCZ) and 1927, C. E. Burt (NMNH). *Wilson County*, Altoona, Neodesha Region, 11 August 1977, Gordon (FMNH). *Woodson County*, Toronto (CAS). *Wyandotte County*, Kansas City (NMNH). Sight records (B. Cutler, in litt. to first author): Butler, Cherokee, Clark, Elk, Trego, and Wabaunsee counties. **LOUISIANA:** *Allen Parish*, 16 February 1963, D. A. Rossman (LSU). *Beauregard Parish*, DeRidder, 1943, E. L. Bell (AMNH); and 41.6 km N Lake Charles, 10–17 August 1941, E. L. Bell (AMNH). *Caddo Parish*, Ida, 11 June 1972, F. H. Eubanks (CAS); Blanchard, 14 February 1967, K. Howard (CAS); and Shreveport,

24 March 1962 (MCZ). *Caldwell Parish*, 10.1 km E Columbia Heights, along LA hwy. 4, 3 April 1966, R. E. Tandy (FSCA). *Claiborne Parish*, Homer, 24 January 1953, N. B. Causey (MCZ). *Evangeline Parish*, Chicot St. Pk., 25 November 1944, W. G. Moore (NMNH). *Grant Parish*, Kisatchie Nat. For., 1 April 1962, G. Pontiff (LSU); Kisatchie Nat. For., Longleaf Vista, no date, T. Yamashita (TY); 5.6 km N Williana, 10 May 1954, H. S. Dybas (FMNH); nr. Williana, 19 October 1953, Dybas (FMNH); and Dry Prong, 9 May 1954, Dybas (FMNH). *Jackson Parish*, Wyatt, 1 September 1941 (AMNH). *Lincoln Parish*, Ruston, 10 July 1950, M. Cazier (AMNH) and 11 April 1960, D. Copeland (CAS); and 8 km E Ruston, 4 January 1961 (LSU). *Rapides Parish*, Alexandria, H. W. Tobias (NMNH); Kisatchie Nat. For., Johnson Tract, 30 December 1958, D. J. Pirone (AMNH); Forest Hill, 11 November 1945, R. L. Wenzel (FMNH); Melder, Fall 1941, E. L. Bell (AMNH); and Camp Claiborne, 28 March 1969, F. C. Rabalais (LSU). *Sabine Parish*, 12.8 km NNW Many, 10 September aa 3 October 1942, E. C. Williams (FMNH). *Vernon Parish*, 6.4 km NE Leesville, 19 April 1962, K. Arnold (LSU); and 4.3 km NE Caney, 8 April 1967, L. D. Wilson (FSCA). **MISSOURI**: *Barry County*, Roaring River St. Pk., 9 May 1936, E. G. Fisher (ANSP); and Washburn, 14 May 1930, H. H. Shamel (NMNH). *Benton Co.*, nr. Warsaw, 0.8 km N jct. MO hwys. 7 & UU, E. G. Riley (UMO); and 4.8 km NW Warsaw, 10 April 1968, J. R. Heitzman (FSCA). *Carter County*, Fremont, 6 January 1942 (CAS). *Christian County*, 2 August 1976, T. J. Riley (UMO). *Cole County*, 9.6 km SE Russellville, 23 March 1958, H. D. Raithoe (CAS). *Hickory County*, 4.8 km E Wheatland, 20 April 1976, R. Sajdak, J. Buday (MPM). *Holt County*, 8 km S Forest City, 12 May 1992, A. P. Bufalino (UMO). *Howell County*, Willow Springs, before December 1959, N. Banks (MCZ). *Iron County*, Graniteville, 20 March 1955, R. E. Crabill (NMNH); 16 km W Ironton, 25 August 1965, R. L. Mondale (CAS); and Ironton, 5 August 1965–31 July 1966, R. L. Mondale (CAS). *Jackson County*, Kansas City, 3 July 1955 (CAS). *Jasper County*, Joplin, Fall 1984 (WDS). *Jefferson County*, Pevely, 23 April 1956, J. M. Kingsolver (INHS). *Madison County*, Fredericktown, 29 July 1967–19 August 1968, R. L. Mondale (CAS). *Miller County*, 3.2 km SE Brumley, 16 June 1967, M. A. Nickerson (CAS). *Moniteau County*, 5 September 1961, E. McDaniel (CAS). *Oregon County*, Alton, May 1956, W. F. Rushton (MCZ). *Phelps County*, Rolla, April 1964, J. R. Waring (AMNH). *St. Clair County*, 16 km NE Osceola, 11 July 1955, P. Anderson (AMNH); and Collins, 17 July 1956 (CAS). *St. Genevieve County*, 6 June 1937 (FMNH); Misplay Glade nr. Co. Rd. DD, no date, T. Yamashita (TY); and St. Genevieve, 31 May 1956, H. A. Lowenstam (INHS). *St. Louis County*, St. Louis, September 1929, P. Paul (NMNH) and 29 March 1963, K. Rhoads (CAS); Glencoe, 25 April 1962, K. Rhoads (CAS); Ranken, 21 July 1929–14 May 1933 and 29 July 1945, E. P. Meiner (NMNH, UMO); Kirkwood

(NMNH); and Eureka, 6-7 March 1963, K. Rhoads (CAS). *Stone County*, 6 October 1973, C. R. Mappes (UMO); N Kimberling City, Table Rock L., Joe Bald area, 25 May 1974, S. E. Thewke (UMO); Notch, 27 August–4 September 1924, A. B. Wolcott (FMNH); and Cape Fair, 14 April 1954, Bagby (MCZ). *Taney County*, Hollister, 19 August 1962, J. C. Johnson (CAS). *Washington County*, Washington St. Pk., 16 May 1943, C. J. Goodnight (AMNH). *County unknown*, Osage Bluff, 1940 (NMNH). **NEBRASKA**: *Thayer County*, Williams, 2 May 1948, Jones & Loomis (FSCA); 4 km N Gilead, 12 July 1982, W. F. Rapp (AMNH, WFR); Gilead, 22 September 1982 and 25 May 1983, Rapp (WFR); and Alexandria, 24 June and 22 September 1982, Rapp (AMNH, WFR). **NEW MEXICO**: *Chaves County*, 11.2 km E Roswell, along Pecos R., 29 July 1956, V. Roth, W. J. Gertsch (AMNH). *De Baca County*, 28.8 km S Taiban, 10 September 1958, D. Hall (CAS). *Dona Ana County*, University Park, 8 July 1967, B. A. Smith (CAS); and Las Cruces, 22 October 1975, T. Schowalter (UGA). *Eddy County*, Carlsbad, 19 June and 21 July 1964, H. T. Hoskins, R. W. Reeves (CAS); Whites City, 24 September 1950 (AMNH) and 5 October 1961, W. J. Gertsch, W. Ivie (AMNH); Carlsbad Caverns Nat. Pk., 1 September 1947 (CAS); and 43.2 km SW Carlsbad, 18-25 July 1964, P. G. Sanchez, R. W. Reeves, P. F. Van Cleave (CAS). *Guadalupe County*, 4.8 km N Vaughn, 18 August 1958, T. Marquez (CAS). *Lincoln County*, 9.6 km W Carrizozo, Malpais Lava Flow, 27 June 1947 (CAS). *Otero County*, La Luz, 10 August 1959, R. A. Miller (CAS). *Quay County*, Ft. Bascoms, now in Tucumcari (NMNH). *San Miguel County*, Las Vegas (INHS), 3 September 1963, L. Nichols, and 13–15 1968, M. Gratten, H. L. Stahnke (CAS); 1.6 km S Las Vegas, 28 September 1965, H. Trujillo (CAS); nr Las Vegas (Hot Spgs.), August 1901, Schwarz (NMNH); and Montezuma, 27 August 1958, W. L. Smith (CAS). *Socorro County*, Mockingbird Gap, S of Oscura Mts., 5 August 1967, C. H. Lowe (AMNH). **OKLAHOMA**: *Alfalfa County*, Cherokee, 6 November 1961, B. Young (CAS), and 8 and 12.8 km S Cherokee, 2 and 18 October 1961, J. Herrington (CAS). *Beckham County*, Sayre (CAS). *Blaine County*, Brown Nose St. Pk., R. L. Landie (OKSU). *Carter County*, Ardmore, October 1954 (CAS). *Cherokee County*, Hulbert, 10 November 1954, R. N. Van Noy (OMNH). *Cimarron County*, 24 km N, 11.2 km W Boise City, 22 June 1966, D. C. Arnold (OKSU). *Cleveland County*, Norman, 7 February 1932, H. Fisher (OMNH), 15 August 1959, J. Ward (MCZ), and 13 October 1975, C. Treaftig (OMNH); and L. Thunderbird, 16 October 1968, R. M. Waering (FSCA). *Comanche County*, Wichita Mtns. Nat. Wildlife Ref., 20 July 1932, H. Fisher (OMNH), 6 June 1939, E. Hixon (CAS), 3 September 1949, C. J. Goodnight (AMNH), 9 March 1963, G. L. Rotramel (INHS), and 30 March 1981, J. M. Carpenter (MCZ). *Craig County*, 15 April 1960, Osume (OKSU). *Dewey County*, 1.6 km N Taloga, along US hwy. 183 at S. Canadian R. 18 April 1980, S. K.

Wu, P. B. LaRochelle (UCO). *Ellis County*, L. Lloyd Vincent, 14 October 1967, D. C. Arnold (OKSU). *Garfield County*, 9.6 km E, 3.2 km S Bison, 20 August 1989, R. L. Landie (OKSU). *Greer County*, Quartz Mtn. St. Pk., 20 September 1952 (NMNH) and 4 June 1954, P. W. Smith (INHS). *Harper County*, 4.8 km N, 3.2 km W Ft. Supply, 22 September 1957, Harper (OKSU). *Haskell County*, Kinto, 4 November 1988, L. Felchick (OKSU). *Hughes County*, 10 December 1933, J. R. Carpenter (OMNH). *Kay County*, Ponca City, 15 October 1975 (OKSU). *Latimer County*, 13 April and 11 June 1931, R. D. Bird (OMNH). *LeFlore County*, nr. Poteau, 16 May 1961 (OKSU). *McClain County*, Johnson's Pasture, 16 February 1935 (OMNH). *Marshall County*, 3.2 km W Willis, along Cowan Cr., 27 June 1958, B. A. Branson (INHS); and L. Texoma, 16 August 1965, B. Rotramel (INHS). *Murray County*, Sulphur, 15–28 June and 20 August 1956 (CAS). *Muskogee County*, 3 August 1978, B. G. Hill (OKSU). *Osage County*, Hulah, 7 May 1985 (MCZ); and Osage Hills St. Pk., 12 October 1985, Blackwood (OKSU). *Pawnee County*, Pawnee, 33 September 1963, M. E. Sisk (OKSU). *Payne County,* Stillwater, 20 November 1990 and 24 November 1963, D. C. Arnold (OKSU) and spring 1970, L. T. Chapin (LSU); and nr. L. Blackwell, 22 March 1990, M. Lee (OKSU). *Pottawatomie County*, Pearson, 26 February 1974, D. C. Arnold (OKSU); and Shawnee, 18 May 1952, J. M. W. (OMNH). *Roger Mills County*, Cheyenne, 5 August 1953, M. C. Sooter (FSCA). *Seminole County,* May 1930 (OMNH). *Sequoyah County*, nr. Sallisaw, 30 June 1961 (OKSU). *Stephens County*, 9.6-11.2 km E Duncan, KX Ranch, 1981, R. E. Knight (MCZ); and Comanche, 15 March 1972, D. C. Arnold (OKSU). *Tillman County*, 14.4 km S Davidson, along Red R., 15 May 1960, M. B. Lamb (OKSU). *Tulsa County*, Tulsa, 1 October 1951 (CAS), and 6 September 1966, R. M. Waering (FSCA). *Woodward County*, vic. Alabaster Caverns St. Pk., 5–11 October 1952 (AMNH). **TEXAS**: Samples were examined which produced the following 59 new county records: Anderson, Angelina, Atascosa, Bandera, Bastrop, Baylor, Brazoria, Brazos, Briscoe, Brown, Burnet, Calhoun, Camp, Cherokee, Comal, Coryell, Ector, El Paso, Fisher, Gray, Harris, Harrison, Hays, Houston, Hudspeth, Hutchinson, Jones, Kendall, Lamar, Lampasas, Leon, Liberty, Llano, Live Oak, Madison, Matagorda, McLennon, Milam, Mitchell, Montague, Moore, Newton, Nolan, Nueces, Palo Pinto, Polk, Potter, Randall, Refugio, Robertson, Runnels, Rusk, San Augustine, Smith, Sterling, Tarrant, Upton, Walker, and Wilbarger (Depositories: AMNH, ANSP, INHS, FMNH, OMNH, SEM, SFASU, TAMU, UGA, UTEP, WDS, WTAMU). Sight records (K. J. McWest, in litt. to second author, 1994): Bell, Callahan, Collin, Eastland, Jasper, Montgomery, Nacogdoches, Rockwall, San Jacinto, and Shelby. These new records and observations bring to 135 the total number of counties in Texas from which *C. vittatus* has been recorded. **MEXICO**: **CHIHUAHUA**: Below

Sierra Ponce, S of Santa Elena (across border from Castolon, Tx.), March 1991, P. Klawinski, P. Monk, R. Truss (SFAU). **COAHUILA**: Saltillo, 23 May 1952, Cazier, Gertsch, Schramme (NMNH); 20 km N Saltillo, 6 Jan 1977, Cokendolpher and Dalquest (MWSU); 40 km N Saltillo, 6 Aug 1972, J. Kaspar (MWSU); Los Pinas, 17.3 km S, 0.2 km E Arteaga, 14 July 1977, Liner, Chaney (FSCA); 24 November 1977, Liner, Bartlett (FSCA); and 17 July 1975, Liner (FSCA). Valle de Guerra, 8.6 km W Bunuelos, 15 July 1977, Liner, Chaney (FSCA). Campo Central, 48 km SE Boquillas (FMNH). 33.6 km NW Ciudad Melchor Muzquiz, 21 July 1972, Liner, Johnson, Chaney (FSCA). Sierra de Penetente, Saltillo to Diamante, 2,340 m, 13 July 1934 (ANSP). Tinajas de Chaves, 32 km S Boquillas, 8 April 1945, K. P. Schmidt (FMNH). **NUEVO LEON**: Km 888 Hualahuises, 10 January 1948 (AMNH). 9.1 km SSW Cerralvo, 14 July 1975, E. A. Liner et al. (FSCA). Montemorelos (FMNH). 32 km N Montemorelos, 16 June 1941, H. S. Dybas (FMNH). Monterrey, 14 June 1941, Dybas (FMNH). 1.0 km S Portrero, Arroyo Mesquital, 16 July 1974, Liner, R. M. Johnson, A. H. Chaney (FSCA). 3.2 km W, 2.2 km S San Antonio de las Alazanas, Cienega del Toro Rd., 24 November 1977, Liner, P. Bartlett (FSCA). 2.2 km SW San Isidro, 22 July 1976, Liner et al. (FSCA). 23 km E San Jose de Iturbide, 21 July 1976, Liner et al. (FSCA). 4.8 km S Galeana, 22 May 1973, D. A. Rossman (FSCA). Picacho Mts., 9.8 km SW, 11.8 km NW Cerralvo, Rancho El Milagro, 11 July 1977, Liner, Chaney (FSCA). 2.9 km E San Juan Batista, 12 July 1977, Liner, Chaney (FSCA). San Juan Batista to La Cienega, Canon San Juan Batista, 15 July 1974, Liner et al. (FSCA). Cienega de Flores, 14 June 1941, Dybas (FMNH). **TAMAULIPAS**: Reynosa, C. C. Hoffmann (AMNH). W of Matamoros, 13 October 1985, H. R. Hermann (UGA). Ciudad Victoria, 17 May 1952 (NMNH) and 17 May 1952, W. J. Gertsch, M. Cazier, R. Schramme (AMNH). Abasolo, 17 May 1952, Cazier, Gertsch, Schramme (NMNH). El Tinieblo, 12 March 1972, B. D. Campbell, R. W. Mitchell (AMNH) and 6 March 1977, R. W. Mitchell (AMNH). Padilla, 17 May 1952, Cazier, Gertsch, Schramme (AMNH). Jimenez, 15 May 1952, Cazier, Gertsch, Schramme (NMNH). La Reforma, 15 October 1984, P. Sprouse (TMM). Sistemica Purificacion, 26 November 1979, P. Sprouse (TMM).

Human importation to others areas.—Specimens that are believed to represent accidental human importations were examined from the following localities. The possibility also exists that some of the specimens below bear erroneous locality data. The specimen from Chicago was encountered in a street, and those from Dare and Wake counties, North Carolina, and Rankin County, Mississippi, were taken in buildings. Juveniles have been collected in Rutherford County, Tennessee, indicating the probable existence of an established, reproducing population (Denise Due, Vanderbilt Univ., pers. comm. to second author, 1981).

CALIFORNIA: *Contra Costa County*, Richmond, August 1952 (CAS). ARIZONA: *Maricopa County*, Phoenix, 22 March 1952, S. Smith (CAS). *County unknown*, Kamah, P. A. Vestal (MCZ). COLORADO: *Boulder County*, Boulder, 8 June 1954 (CAS). IOWA: *County unknown*, Missouri Valley, 4 August 1941 (CAS). MISSOURI: *Clark County*, Fairmont (CAS). ILLINOIS: *Cook County*, Chicago, 3 June 1922, M. Jensen (FMNH). *McHenry County*, Woodstock, October 1951 (CAS). KENTUCKY: *Marshall/Calloway Counties*, Kentucky L., 15 August 1975 (INHS). TENNESSEE: *Rutherford County*, Tiger Hill nr. Murfreesboro, November 1981 (WDS). *Shelby County*, Memphis, 13 August 1955 (CAS), and January 1963, O. E. Smith (CAS). LOUISIANA: *East Baton Rouge Parish*, Baton Rouge, November 1962, T. B. Murrell (LSU) and 12 October 1983, M. Villars (LSU). *Orleans Parish*, New Orleans, 31 July 1962, P. Esteve (CAS). *County unknown*, Mississippi River (NMNH). MISSISSIPPI: *Lamar County*, nr. Sumrall, summer 1989 (MMNS). *Pike County*, Summit, September 1966, J. D. Smith (CAS). *Rankin County*, Brandon, 7 August 1990, B. Tanner (MEM). NORTH CAROLINA: *Dare County*, Nags Head, 10 May 1986, L. Griffin (NCSU). *Nash County*, Rocky Mount, 26 July 1991 (NCSM). *Wake County*, Research Triangle Park, August 1991 (NCSM); and Raleigh, Wakefield St., 24 October 1986, M. A. Brittain (NCSU) and Bland Rd., 13 May 1991, J. Wigmore (NCSM).

It is also noteworthy that *C. vittatus* may have been introduced abroad as well. At least, there are some specimens in museum collections bearing labels from locations in South America. Sissom & Lourenço (1987) discovered that the species *C. dasypus* Mello-Leitão described from Andahuaylas, Peru was in fact *C. vittatus*. These specimens were probably mislabeled, as the locality is deep in the mountainous interior of the country. There are also several specimens of *C. vittatus* from Caracas, Venezuela in the Field Museum of Natural History, Chicago.

Centruroides hentzi (Banks)
Figs. 3, 5, 6, 7

Habitat.—According to Muma (1967), *C. hentzi* usually occurs under litter, logs, and stones in Florida; it can also be found under bark of dead trees and often enters houses. North of Florida, specimens were encountered under pine and oak bark in Camden and Charlton counties, Georgia, respectively, and inside houses, condominiums, or dormitories in Charlton County, Georgia; Charleston County, South Carolina; and Durham, Carteret, and Brunswick counties, North Carolina. Of the six specimens seen at the South Carolina site, two have been preserved, one of which was in a sleeve of a robe and stung

the collector when she tried to put on the robe (Langley 1994).

Distribution.—In the United States, *C. hentzi* was previously known only from Florida, where it occurs statewide (Muma 1967); it can now be reported from adjacent parts of Alabama and Georgia, where it would logically be anticipated (Figs. 6, 7). In Georgia, the scorpion appears to be common in the southern tier of counties adjacent to Florida; it occurs offshore on Cumberland Island, and these specimens constitute topotypes of *Buthus vittatus* Say. The westernmost locality, Mobile, Alabama, establishes *C. hentzi* west of the Alabama River and suggests eventual discovery in southeastern Mississippi. Specimens from outside of Florida that are believed to represent natural occurrences were examined from the following localities:

ALABAMA: *Baldwin County*, Bon Secour Nat. Wildlife Ref., along AL hwy. 180 ca. 19.2 km W Gulf Shores and 41.6 km W Florida State/Escambia County line, 17 April 1993, R. L. Brown (MEM); and Josephine, 29 December 1993 (NCSU). *Mobile County*, Mobile, H. P. Loding (AMNH). GEORGIA: *Camden County*, private land on Cumberland Island, 25 December 1993, C. Ruckdeschel, C. R. Shoop (CIM, NCSM, NMNH, WDS). *Charlton County*, 6.4 km W Folkston, 19 March 1936, F. Harper (NMNH); and Okefenokee Natl. Wildlife Ref., 13 June 1981, C. L. Smith, S. N. Brown (UGA) and Billy's Island, 29 January 1978, D. H. Habeck (FSCA). *Clinch County*, 22.4 km N Fargo, 25 December 1949, Smith & Smith (INHS). *Cook County*, Adel, Fall 1937, J. T. Dampier (NMNH). *Lowndes County*, 4.8 km NW Valdosta, March 1976, D. Daleske (FMNH). *Mitchell County*, 6.4 km N Sale City, 27 November 1949, J. W. Crenshaw (FSCA). *Thomas County*, 20 April 1973 and 6 January 1976, W. T. Sedgwick (MCZ); Thomasville, 9 December 1903, M. Hebard (ANSP), March 1939, J. White (FMNH) and May 1942, E. Ireland (FMNH); 16 km S Thomasville (Birdsong Plantation), 15 April 1945, D. C. Lowrie (FMNH); and Millpond Plantation, 3 March 1973 (MCZ). *Ware County*, Waycross, 8 May 1937, T. H. Hubbell (CAS); 16 km SE Waycross, 16 March 1963, H. W. & L. R. Levi (MCZ); and Laura Walker St. Pk., 19 February 1988, W. E. Steiner, J. B. Stribling (NMNH). *County unknown*, Clermont, 21 June 1955, A. W. Vasquez (NMNH).

Human importation to other areas.—Specimens that are believed to represent accidental human introductions were examined from the following localities. The samples from Georgia could conceivably represent natural occurrence because these two counties, in the Fall Zone and outer periphery of the Piedmont Plateau, ca. 160 km from the most proximate locality, are not so remote as to be implausible indigenous records, par-

ticularly if *C. hentzi* occurs northward in the Gulf Coastal Plain.. However, they are detached from the clustered and unquestionably native records in southern Georgia and are therefore treated as introductions. The specimens from South Carolina and Brunswick County, North Carolina, were possibly imported with Florida palm trees that have been planted along the coast of the Carolinas (J. Morse, pers. comm). Reproducing populations have not been verified at any of the following sites.

GEORGIA: *Harris County*, 10 May 1970 (CC). *Muscogee County*, Columbus, 17 May 1959 (CC). **NORTH CAROLINA:** *Brunswick County*, Bald Head I., February 1993 (NCSM) and 1.6 km E of Marina, July 1992 (RNH). *Carteret County*, Bogue Banks, Emerald Isle, September 1993, D. McLuskey (NCSM). *Durham County*, Duke Univ., 8 September 1987, C. Brock (NCSU). **SOUTH CAROLINA:** *Charleston County*, Isle of Palms, 20 February 1994, S. Mims (NCSM).

COMPARISON OF SCORPION DISTRIBUTIONS IN THE EASTERN UNITED STATES

The known indigenous distributions of the scorpions in the United States east of the Central Plains are compared in Fig. 7; the ranges of *C. gracilis* and *C. guanensis* (= *C. keysi*), and *V. carolinianus* are adapted from maps published by Muma (1967) and Shelley (1994a), respectively. There is no known overlap between *V. carolinianus* and any of the buthids, although its range is only about 112 km north of that of *C. hentzi* in southern Alabama. According to Muma (1967), *C. guanensis* is restricted to Collier, Dade, and Monroe counties, Florida. *Centruroides gracilis* is indigenous to the peninsula from Alachua County southward. To our knowledge, these distributions are still current, but we did discover the following two samples of *C. gracilis*, representing accidental human importations, from well outside this area.

MISSISSIPPI: *Rankin County*, in concrete debris at truck stop on US hwy. 49 just S I-20, nr. Jackson, 27 October 1983, E. S. Olson (MMNS). **TEXAS:** *Galveston County*, Galveston, 1935 (NMNH).

Additionally, there is an invididual of *C. gracilis* from Dallas, Texas (NMNH), that was taken in 1956 "in produce from Central America," and another collected in 1930 on a ship berthed at New Orleans (NMNH).

ACKNOWLEDGMENTS

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NATURAL HISTORY OF THE SPIDER GENUS *LUTICA* (ARANEAE, ZODARIIDAE)

Martin G. Ramirez: Department of Biology, Bucknell University, Lewisburg, Pennsylvania 17837 USA

ABSTRACT. Spiders of the genus *Lutica* are fossorial inhabitants of coastal dunes of southern California, Baja California and the California Channel Islands. They live in silk-lined burrows concentrated beneath dune vegetation. *Lutica* are sit-and-wait predators that subdue insects that walk near or over burrows. They are sedentary and do not engage in aerial dispersal via ballooning. Adult males abandon their burrows during the late summer and early fall to wander in search of females. Females produce eggsacs and guard them till they die; spiderlings emerge in the spring. Dune trapdoor spiders (*Aptostichus simus*) prey on *Lutica*, while the larvae of a therevid fly are external parasites.

Spiders of the genus *Lutica* are fossorial inhabitants of coastal dunes of southern California, Baja California and the California Channel Islands (Gertsch 1961, 1979; Ramirez 1988). Although described over 100 years ago (Marx 1891), little is known of their natural history. Gertsch (1979) stated that they are nocturnal and come to the surface at night to hunt various beetles and other insects that drop on the sand, and that they spin a loose tubular retreat deep in the cool, moist sand. Gertsch (1961) believed that they probably live for two to three years, with males maturing in the summer or fall, but admitted that little was known about the details of the "... lives and habits of these large, whitish spiders."

George Marx first described the genus *Lutica* from Klamath Lake, Oregon (Marx 1891). Gertsch (1961) corrected the type locality of *Lutica maculata* to Santa Rosa Island, California, and also described three new species: *nicolasia* (San Nicolas Island), *clementea* (San Clemente Island) and *abalonea* (Oxnard, Ventura County). Additional species have been described from India (Tikader 1981), but these taxa are clearly misplaced (Jocqué 1991). Gertsch (pers. comm.) has prepared a revision of *Lutica* based on morphological features, while Ramirez & Beckwitt (in press) have re-defined valid species and determined their phylogenetic relationships based largely on molecular characters. Since these works propose very different species designations than Gertsch (1961), species names in *Lutica* are uncertain at this time.

My study of *Lutica* elaborates on the natural history of this obscure genus.

METHODS

From 1982 to 1987, I collected over 3000 *Lutica* from 20 different dune systems in southern California and Baja California (Fig. 1), including sites on all the Channel Islands except Anacapa (where they are not known to exist), as part of a study of the population genetics and biochemical systematics of this genus (Ramirez 1990). Spiders were collected by sifting dune sand beneath beach vegetation using geologic sieves with a minimum mesh size of 1.0 mm. All specimens were brought back to the laboratory alive, where they were either used for observations or processed for starch gel electrophoresis. Living spiders were maintained in small upright glass or plastic containers or in horizontal glass tubes, partly filled with beach sand. Water was added periodically with either an eye dropper or atomizer. I fed them small arthropods, mainly fruit flies, house flies and beetle larvae (wireworms).

For a mark-recapture experiment with *Lutica* in the field, I marked spiders on the dorsal surface of their abdomens with quick drying scale model paint (Testors Flat White), after first cooling the spiders in a refrigerator for 30 min to make them sluggish and easier to mark. After the spiders were warmed to ambient temperature, there was no visible difference in their behavior.

RESULTS

Burrow construction. — Individual *Lutica* readily constructed burrows in the laboratory after being placed in sand-filled containers. Burrows consisted of silk-lined tunnels in the sand,

usually just below the surface and sometimes partly against the side of the glass container. This facilitated the observation (under subdued light) of activities within. Burrows had either open entrances or no entrances.

On two occasions, I observed burrow construction. In one case, the horizontal glass tube occupied by the spider was packed with moist sand in the sealed end. The spider moved about in a space between the sand and the lower side of the glass tube (Fig. 2). It moved its spinnerets from side to side and up and down, cementing fragments of sand together with silk, and slowly moved in a circle as it did so. It sometimes stopped this activity and moved over to the interior of the burrow wall where it pushed forward with its forelegs, pushing back the wall and expanding the burrow. It then resumed its circular spinning activity. I observed the spider until it suddenly halted its activity and did not resume work on its burrow. In the second case, also with a spider in a horizontal glass tube, the spider half-carried, half-pushed a pile of sand toward the entrance of its burrow. Before it reached the entrance, it halted its activities and did not continue.

In the field, burrows were concentrated in and about stands of native dune vegetation, particularly *Abronia maritima* and *Franseria chamissonis*, and extended into the dune amidst litter and the root systems of the plants. On Santa Barbara Island, typical coastal dunes do not exist and these spiders live in the sandy soil and debris below vegetation growing on a sea cliff. While burrow entrances were normally not visible, one could often see small dimples on the open surfaces of vegetated dunes after strong winds. These usually proved to be the entrances of *Lutica* burrows, composed of a delicate sand-covered, flap-like lid; this is consistent with Thompson's (1973) description of burrows on Santa Cruz and San Miguel Islands. Most burrows descended into the sand at about a 45° angle, although some had portions of their length laying horizontally, just below the sand surface. On the other hand, at La Jolla Beach (Ventura County), I found four burrows that descended vertically into the sand. *Lutica* burrows were usually very fragile and quickly fell apart if the sand around them was removed. Individual burrows were usually from 2.5–15 cm in length, though W. Icenogle and I found a burrow that was 25–30 cm long (occupied by a mature female) at Little Harbor, Santa Catalina Island.

Figure 1.—Map of southern California and Baja California, including the Channel Islands, showing *Lutica* sample sites. Population abbreviations are as follows: Channel Islands - Cuyler Harbor, San Miguel Island (SMI); Southeast Anchorage, Santa Rosa Island (SRI); Johnstons Lee, Santa Cruz Island (SCI); cliffs south of Signal Peak, Santa Barbara Island (SBI); Army Camp Beach (SNA), Dutch Harbor (SND), Red Eye Beach (SNE), San Nicolas Island; Little Harbor, Santa Catalina Island (CAT); Flasher Road Dunes, San Clemente Island (SCL); Mainland - Coal Oil Point Reserve (COP), Santa Barbara Co., California; McGrath State Beach (MG), Ventura Co., California; Oxnard Beach (OX), Ventura Co., California; La Jolla Beach (LJB), Ventura Co., California; Ballona Wetlands (BA), Los Angeles Co., California; El Segundo Dunes, LAX (ESG), Los Angeles Co., California; Balboa Beach (NB), Orange Co., California; Ponto State Beach (PON), San Diego Co., California; Silverstrand State Beach (SVS), San Diego Co., California; Punta Estero (PE), Baja California Norte, Mexico; Guerrero Negro (GN), Baja California Sur, Mexico.

Prey capture.—Once they had constructed burrows in the laboratory, the spiders readily accepted small insects as food. An insect crawling about on the surface of the sand elicited an immediate response. The spider (hanging upside down) would rush about on the "ceiling" of its burrow, possibly trying to locate the exact position of the insect by the vibrations caused by its activities. If the insect suddenly ceased its
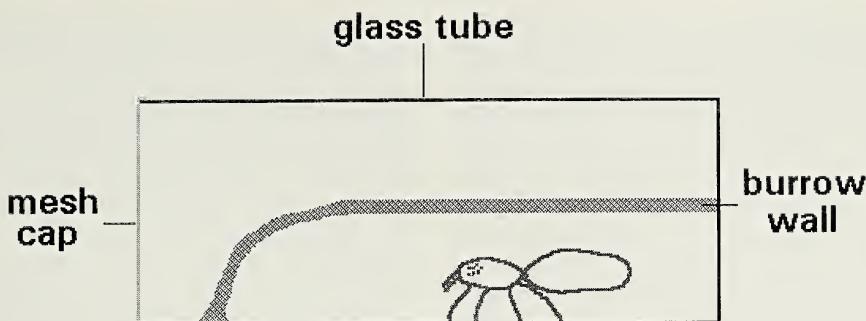
Figure 2.—Profile of horizontal *Lutica* rearing container, showing the orientation of a spider and its burrow. Containers were 2.5 cm in diameter and 9.5 cm long.

movements, the spider would likewise stop its movements and would remain motionless until the insect started moving once again. Once the spider had positioned itself below the insect, it would lunge up and through the wall of the burrow, grab the insect and pull it inside the burrow. Spiders sometimes left their burrow completely to pursue prey that initially escaped; they brought the prey back to the burrow either through the open entrance or through the hole created in leaving the burrow. Once insects ceased to struggle inside the burrow, the spider would leave the insect to patch up the hole in the burrow wall, and would then return to feed on the now dead prey.

While the capture of prey through the burrow wall was typical, spiders sometimes emerged from their burrows at the first sign of prey vibrations and subdued their prey directly, before taking them inside the burrow. Most spiders deposited the prey remains outside the burrow following feeding. Field-collected burrows were always uniformly clean and a prey item was found inside a burrow on only one occasion.

Timing of reproduction.—*Lutica* males molt to maturity and abandon their burrows to wander about in search of females. Based on a master list of collecting records of all *Lutica* specimens (available on request), the earliest record of an adult male is May 11 (1♂, Oxnard Beach, Ventura County, 1968, M. Thompson) and the latest records are November 3 (1♂, Oxnard Beach, Ventura County, 1982, M. Ramirez) and November 4 (1♂, Silverstrand State Beach, San Diego County, 1982, M. Ramirez). The largest number of records and actual numbers of males collected are for September and October. For example, pitfall traps set up in dunes at Pt. Mugu Naval Air Station, Ventura County collected 169 adult

male *Lutica* between 31 August–18 October 1981 (C. Nagano & J. Donohue pers. comm.). Thus, the peak of the breeding season appears to be late summer and early fall.

Following mating, females produce eggsacs, though how soon is not known; there then follows the period of spiderling growth and development. My earliest record of brood spiderlings was 15 April (El Segundo Dunes, Los Angeles International Airport, Los Angeles County, 1985), and I collected broods as late as August from both island and mainland populations. Females presumably guard eggsacs and young till they die; of 22 eggsacs or broods collected in 1985 and 1987, 12 were found in burrows along with the shrunken remains of adult females. Since burrows are destroyed during collection, scattering their contents, it is probable that the remains of adult females also may have been present with the other 10 eggsacs/broods.

Dispersal.—Mark-recapture data suggest that non-reproductive dispersal is limited. At Coal Oil Point Reserve (Santa Barbara County), 170 spiders from a single dune were captured on 28 February 1984, marked on the dorsal surfaces of their abdomens and released into the dune from which they were taken. Seventy-seven (45.3%) of 170 spiders collected at that same dune a month later were marked. Assuming the loss of marks by individual spiders due to molts in the intervening period, actual site fidelity was probably greater. However, since I did not have an opportunity to collect in dunes adjacent to the one in which the marked spiders were released, it is not known how many of the marked spiders I failed to recover may have moved to different dunes in the intervening month. Nonetheless, since their burrows were destroyed when the spiders were first collected, it is remarkable that

such a large percentage of them stayed in the same dune following release.

Gertsch (1961) stated that *Lutica* do not balloon, as is common among many spiders (Decae 1987), and *Lutica* of all sizes instantly buried themselves in the sand if removed from their burrows. However, while sifting for *Lutica* during Santa Ana wind conditions, I often saw small specimens cling tenaciously to the mesh of the sieve; if they lost their grip, the smallest spiders would sometimes be blown up and out of the sieve. This is a highly unnatural situation, since the spiders do not normally move about at the surface during the day and would certainly not find themselves a foot or more above the sand surface. Dune vegetation is prostrate and I have never seen them climb about in plants. On the other hand, twice during Santa Ana winds, I saw a few immatures and adult females moving about on the surface of the dunes. Since I never observed *Lutica* moving about on the surface on any other occasions, it is possible that the wind had shifted the sand in the area where these spiders had made their burrows, eventually dislodging them. Thus, while they do not engage in ballooning behavior, it may be possible for the smallest instars of *Lutica* to be carried away in high winds.

Predators. — Trapdoor spiders of the genus *Aptostichus* (Cyrtaucheniidae) are the only organisms known to prey on *Lutica*. One member of this genus, *A. simus*, is restricted to coastal dunes in southern California (Chamberlin 1917), including the California Channel Islands, and it lives in silk-lined burrows. In September 1979, W. Icenogle (pers. comm.) found the remains of an adult male *Lutica* (as well as an adult male *Aptostichus*) in the burrow of an adult female *Aptostichus* in a coastal dune near Encinitas, San Diego County. Since only adult male *Lutica* would normally be expected to wander about on the surface of the sand, it is not likely that *Aptostichus* prey on non-male *Lutica*.

Parasites. — Of the thousands of *Lutica* collected over six years, only a single spider was parasitized. In September 1983, I collected three *Lutica* from La Jolla Beach (Ventura County) which were paralyzed. Attached to the abdomen of one of the spiders was a small white larva. The larva eventually consumed the spider from the outside in, but unfortunately died without pupating. E. Schlinger (pers. comm.) identified the larva as that of a therevid fly (Diptera). No Therevidae have been reported previously as spider parasites (Eason et al. 1967; E. Schlinger pers. comm.).

Prey. — In the field, I recovered many *Lutica* with beetle larvae (wireworms) in their chelicerae and found one burrow which contained the dry remains of a wireworm. In the laboratory, *Lutica* readily attacked any small insects or spiders and never rejected any arthropod they were capable of subduing. If many prey items were supplied at once, most *Lutica* attacked and subdued all the arthropods in rapid succession before they began to feed on any of them.

DISCUSSION

Burrow construction. — The fossorial lifestyle of *Lutica* is typical of the Zodariidae, most of which are ground or forest floor dwellers which often construct silken retreats, either burrows or silk-lined bags (Jocqué 1991, 1993). Aside from *Lutica,* the construction of burrows with trapdoors has been reported among the Zodariidae in *Antillorena* (Gertsch 1961; Jocqué 1991), *Capheris* (Hewitt 1914; Jocqué 1991), *Neostorena* (Jocqué 1991) and *Psammorygma* (Jocqué 1991, 1993). Observations of burrow construction have not been reported previously for a zodariid, although Harkness (1977) detailed the construction of a bag-type shelter by *Zodarion frenatum.*

Prey capture. — The prey capture behavior in *Lutica* described herein is the first description of the sub-surface attack sequence of a burrow-dwelling zodariid. Since the orientation of burrows in the field ranged from nearly horizontal to vertical, it is probable that the sub-surface attack sequence described for *Lutica* only applies to those burrows which have at least some portion lying near the surface in a horizontal position, where arthropods can walk across them. With burrows situated at steeper angles, *Lutica* probably come out to attack passing insects, as did some laboratory spiders and as does *Antillorena* (Gertsch 1979).

The sub-surface prey location and attack behavior of *Lutica* strongly parallels that reported for the "purse web" spiders, *Atypus, Calommata* and *Sphodros* (Atypidae) (Bristowe 1958; Coyle 1986). These three spiders are all burrow dwellers which construct a tube-like, silken extension of the burrow (the "purse web") that extends along the ground or vertically against a tree or other support. Prey are located when they walk or land on the purse web: the spider locates the position of the prey by its vibrations and once

positioned below the insect, it then strikes through the silken tube, slits open the purse web and pulls the prey inside, much as *Lutica* does in its own burrows. However, while only the fangs of purse web spiders are extended though the tube wall to capture prey, *Lutica* may force much or all of its body through the burrow wall to do so. This similarity in attack sequence may be an example of convergence in behavior involving spiders in two very different families, due to the functional similarities of a purse web and a shallowly buried silk-lined burrow.

Timing of reproduction.—The presence of males in the field largely in the summer and fall, coupled with the appearance of spiderlings by the spring, indicates that the production of eggsacs and development of young takes place sometime between fall and spring. Bonnet (1935) noted that many spiders which mature and mate toward the end of the summer produce overwintering eggsacs in the fall, with spiderlings emerging in the spring. Since brood spiderlings were collected in the field as early as April, it would appear that production of eggsacs and subsequent development of spiderlings is consistent with that of other spiders which mature in the late summer. When *Lutica* do reproduce, it is probable that the females guard the eggsacs and developing spiderlings in their burrows till they die, as evidenced by the regular collection of eggsacs or broods along with the remains of adult females.

Dispersal.—Given the isolation of coastal dune systems along the southern California and Baja California coasts (Fig. 1) (Cooper 1967; Powell 1981), knowledge of the extent and timing of inter- and intra-dune dispersal by *Lutica* would be of great value in understanding the structure of their populations and patterns of genetic variation within and among them (Ramirez 1990). On a local scale, a low dispersal rate among different parts of a dune system [typical size 2–10 km² (Powell 1981)] might lead to genetic subdivision, and possibly the evolution of microgeographic races (Doyen & Slobodchikoff 1984).

The results of the mark-recapture study suggest that non-reproductive terrestrial dispersal is low. Terrestrial dispersal is probably limited to wandering males and those spiders dislodged from their burrows by the shifting of dune sand. Nonetheless, dispersal on a local scale is apparently effective enough to maintain genetic homogeneity among spiders in dunes on the same beach (Ramirez 1990).

Ballooning is rare in fossorial spiders (Decae 1987) and has never been reported in the family Zodariidae (Jocqué 1993). However, Robinson (1982) has suggested that spider aerial dispersal may sometimes be accidental. More specifically, if a spider is small and light, it is possible that if it loses its hold of the substrate while exposed to wind of sufficient strength, it might become airborne solely due to its favorable aerodynamic characteristics (Glick 1939). This apparently happened with small *Lutica* in my sieves during Santa Ana winds. However, since ballooning spiders depend on wind borne silk threads for lift (Coyle 1983), it is unlikely that *Lutica* travel far even if they do become airborne, since they were never seen to pay out threads of silk into the wind or drop from elevated positions on draglines exposed to the wind, the two means spiders use to accomplish ballooning (Coyle 1983; Decae 1987).

If aerial transport is a regular means of *Lutica* dispersal, one would expect that there would be few dune systems that they would not be capable of invading; yet, they are absent from most of the coastal region between Ventura County and Los Angeles (their absence from the well developed dune system at Pt. Dume is particularly puzzling) and from Anacapa Island, the closest of the Channel Islands to the mainland (Fig. 1). Although Anacapa has no dune system, *Lutica* live on much more isolated Santa Barbara Island in a non-dune habitat. Thus, while it may be physically possible for *Lutica* to become airborne, it is not likely that such a means of dispersal has played a large part in creating present distributions.

Predators.—Among the small but distinct arthropod fauna of California coastal dunes (Nagano 1981; Powell 1981), *Lutica* and *Aptostichus simus* are the only predators to occupy silk-lined burrows. The record of a male *Lutica* from an *Aptostichus* burrow is not unexpected, since their burrows are often found side by side in the dunes. While no other case of predation on *Lutica* was observed, there are a few invertebrate and vertebrate insectivores that occupy California coastal dunes and may potentially feed on *Lutica*, specifically windscorpions (Solpugida), side-blotched lizards (*Uta stansburiana*) and California legless lizards (*Anniella pulchra*) (Hayes & Guyer 1981; Nagano et al. 1981). However, such potential predators were only rarely encountered while collecting *Lutica*.

Parasites.—The record of a therevid fly larva

consuming a paralyzed *Lutica* is highly unusual. Therevid larvae are predators of sand dune inhabiting insects and some may specialize on tenebrionid larvae (Doyen 1976, 1984). Their interactions with spiders have not been reported previously. Spider wasps (Pompilidae), which are abundant in southern California, are spider specialists and typically paralyze their prey (Wausbauer & Kimsey 1985), so the three paralyzed spiders found at La Jolla Beach (Ventura County) were presumably the result of pompilid activity. If these spiders were indeed attacked by pompilid wasps, the absence of wasp eggs or larvae attached to the paralyzed bodies is puzzling; perhaps they were knocked off during sifting. The presence of a therevid larva attached to one of the three paralyzed spiders was probably the result of a chance encounter with the immobile spider during the larva's movements through the sand.

Prey.—Tenebrionids (Coleoptera) and their larvae (wireworms) are among the most abundant insects in California coastal dunes (Doyen 1976, 1984) and their numbers far exceeded the numbers of other insects recovered during sifting. Both Gertsch (1961) and Thompson (1973) suspected that *Lutica* preyed on tenebrionids and my capture of many of them with wireworms in their chelicerae has proven them correct. However, save for the chance collection of *Lutica* with prey items, it will be difficult to determine whether *Lutica* prey on adult beetles (or any other organisms), given their rapid disposal of prey remains upon completion of feeding. The application of electrophoretic (Murray & Solomon 1978; Fitzgerald et al. 1986) and serological (Greenstone 1977; Southwood 1978) analyses might distinguish, from a range of possible prey items, what *Lutica* are actually eating.

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REDESCRIPTION OF THE PENNSYLVANIAN TRIGONOTARBID ARACHNID *LISSOMARTUS* PETRUNKEVITCH 1949 FROM MAZON CREEK, ILLINOIS

Jason A. Dunlop: Department of Earth Sciences, University of Manchester, Manchester M13 9PL, UK

ABSTRACT. The holotypes of the trigonotarbids *Lissomartus carbonarius* (Petrunkevitch 1913) and *Lissomartus schucherti* (Petrunkevitch 1913) (Arachnida, Trigonotarbida) from the Pennsylvanian (Westphalian D) of Mazon Creek are redescribed. These forms may be synonymous, representing male/female or juvenile/adult dimorphs, but the two species are retained at present. A new reconstruction of *Lissomartus schucherti* is presented. A new family, Lissomartidae, is proposed for these species based on a combination of their lack of opisthosomal tuberculation and their opisthosomal segmentation pattern of tergites 2 + 3 fused and tergite 9 divided into median and lateral plates. Lissomartidae new family may be intermediate between Trigonotarbidae and Eophrynidae + Aphantomartidae.

Trigonotarbid arachnids ranged from the Upper Silurian (Přídolí) (Jeram et al. 1990) to the Lower Permian (Asselian?) (Scharf 1924). Superficially spider-like animals, they lack silk-producing spinnerets, and are characterized by an opisthosoma with tergites divided into median and lateral plates. Trigonotarbids have been placed in the arachnid taxon Tetrapulmonata Shultz 1990, as the plesiomorphic sister group of the orders Araneae, Amblypygi, Uropygi and Schizomida (Shear et al. 1987). Trigonotarbids are most numerous in the coal deposits of North America and Europe and two specimens from Mazon Creek are redescribed here and interpreted as cursorial predators on other arthropods. These specimens represent two species in a single genus, which is placed in a new family.

PREVIOUS WORK

One of the most productive areas for trigonotarbid fossils is the Pennsylvanian (Westphalian D) locality of Mazon Creek, Illinois. Petrunkevitch (1913) described two new arachnids from Mazon Creek (in what was then the order Anthracomarti): *Trigonotarbus schucherti* and *Trigonotarbus carbonarius*. The genus *Trigonotarbus* Pocock 1911 was rediagnosed by Petrunkevitch (1913) as trigonotarbids having a triangular carapace, lacking ornamentation, with a raised median region. Petrunkevitch (1913) differentiated *T. schucherti* from *T. carbonarius* and Pocock's type species, *T. johnsoni* from the Westphalian B of the British Middle Coal Measures, on account of the coxae touching along the mid-

line in *T. shucherti* and coxae separated by a sternum in the other two species. He differentiated *T. carbonarius* from *T. johnsoni* by the shape of the sternite surrounding the anal operculum (a structure now interpreted as a pygidium, see below).

In 1949 Petrunkevitch created a new genus, *Lissomartus*, for *T. schucherti* and *T. carbonarius*. He created a new family, Trigonotarbidae, for *T. johnsoni*, but placed his new genus *Lissomartus* in the family Trigonomartidae, a substitute name for the family Aphantomartidae, proposed earlier by Petrunkevitch (1945). Petrunkevitch (1949) also created the order Trigonotarbi for some of the anthracomartid material, including *Lissomartus* (see Shear et al. (1987) for a discussion).

Petrunkevitch (1949) diagnosed the family Trigonotarbidae as having an eight-segmented opisthosoma with the terminal tergite not divided into median and lateral plates, while the Trigonomartidae was diagnosed as having an eight-segmented opisthosoma with a terminal tergite which was divided into median and lateral plates. It was on these grounds that *Lissomartus*, with a divided terminal tergite, was placed in the Trigonomartidae. The genus *Lissomartus* was defined by Petrunkevitch (1949) as trigonomartids with a smooth carapace and opisthosoma, the carapace being subtriangular, longer than wide and concave on each side anteriorly. This interpretation and systematic placement was retained by Petrunkevitch (1953, 1955) in his two further major reviews of the Trigonotarbida. The family

name Trigonomartidae was rejected in favor of the original name, Aphantomartidae, by Selden & Romano (1983). A reappraisal of *L. carbonarius* and *L. schucherti* was deemed necessary in the light of misinterpretations in Petrunkevitch's morphological and taxonomic work (e. g., Selden & Romano 1983; Shear et al. 1987).

METHODS

The holotypes of *Lissomartus schucherti* (Peabody Museum, Yale University (YPM), specimen no. 169), and *L. carbonarius* (United States National Museum, Washington DC (USNM), specimen no. 37978) were whitened with ammonium chloride and studied under a binocular microscope. Drawings were prepared with the aid of a camera lucida. Both specimens are from Mazon Creek, Illinois, USA, which is dated at Pennsylvanian (Westphalian D) in age (see Nitecki 1979 for a geological interpretation of this locality).

The holotype (British Museum, Natural History (BMNH) In 31239), of *Trigonotarbus johnsoni* and other specimens of this species were studied as the type and only species of the family Trigonotarbidae. The holotypes of *Aphantomartus areolatus* (British Geological Survey (GSM) 25016–7) and *Trigonomartus pustulatus* (USNM 37984), were studied as representatives of the family Aphantomartidae. The holotype of *Eophrynus prestvicii* from the (Lapworth Museum, Birmingham University, UK (BU) 699) was studied as a representative of the Eophrynidae.

MORPHOLOGICAL INTERPRETATION

Both specimens of *Lissomartus* are preserved as external molds in clay-ironstone nodules. YPM 169 (Figs. 1–4) consists of part and counterpart showing the dorsal and ventral surfaces of the animal respectively, while USNM 37978 (Figs. 5, 6) consists of one half of a nodule only, the counterpart being unknown from the time of the original description, and shows the ventral surface.

The carapace of YPM 169 (Figs. 1, 3, 7) shows the approximately triangular shape characteristic of many trigonotarbids, with a raised median region bearing a pair of eyes on a single tubercle. Additionally this median region also bears a pair of oval tubercles on this raised median region either side of the eye tubercle, and two less well defined tubercle pairs posterior to the eye tubercle, comprising a round and an elongate tubercle pair respectively.

Some Devonian trigonotarbids show multi-faceted lateral eye tubercles in addition to the median eye tubercle (e. g., Shear et al. 1987), and it is conceivable that the oval tubercles either side of the eye tubercle in YPM 169 are lateral eye tubercles, too. However, since lateral eye tubercles are not present in any of the other taxa interpreted as closely related to *Lissomartus* and would represent an uncharacteristically plesiomorphic character in an otherwise rather derived trigonotarbid, I prefer to interpret these, with reservations, as simple tubercles (Fig. 7), as are observed in greater density on the carapaces of the eophrynids and aphantomartids.

The opisthosomal morphology of the Pennsylvanian trigonotarbids is interpreted in comparison with the superbly preserved Devonian Rhynie chert material (Dunlop 1994). Interpretation of the Rhynie chert material indicates that trigonotarbids have an opisthosoma of 12 segments with 9 dorsal tergites, the first of which is modified into a locking ridge which tucks under the carapace and is often very small (Dunlop 1994). Tergites 2 and 3 are fused into a single macrotergite in most trigonotarbids (Selden & Romano 1983; Shear et al. 1987). The last two segments (11, 12) are ring-like and form a pygidium, with segment 10 forming a plate, not divided into tergites and sternites, surrounding this pygidium (Figs. 4, 7).

Ventrally, sternite 1 is interpreted as being absent in trigonotarbids (Dunlop unpubl. data). In comparison with Recent tetrapulmonate arachnids (Shultz 1993) 'sternites' 2 and 3 (the two anteriormost ventral sclerites in trigonotarbids) probably represent highly derived sutured-on lung-bearing appendages and are termed the anterior and posterior operculae respectively (Shultz 1993). Sternite 4 is therefore the first visible true sternite in trigonotarbids. Applying this interpretation to *Lissomartus*, its dorsal opisthosomal segmentation (Figs. 1, 3, 7) shows a first tergite without lateral plates, interpreted as the locking ridge which would have tucked under the carapace in life, and then subsequent divided tergites indicating a fused macrotergite 2 + 3. Tergite 9 is divided, but the division is not as strong as on the preceding tergites.

Ventrally, in YPM 169 (Figs. 2, 4), there is a raised, bilobed structure apparently on the anterior operculum. This is unusual among trigonotarbids, which normally bear a similar raised structure on the posterior operculum. The bilobed structure is interpreted as being homolo-
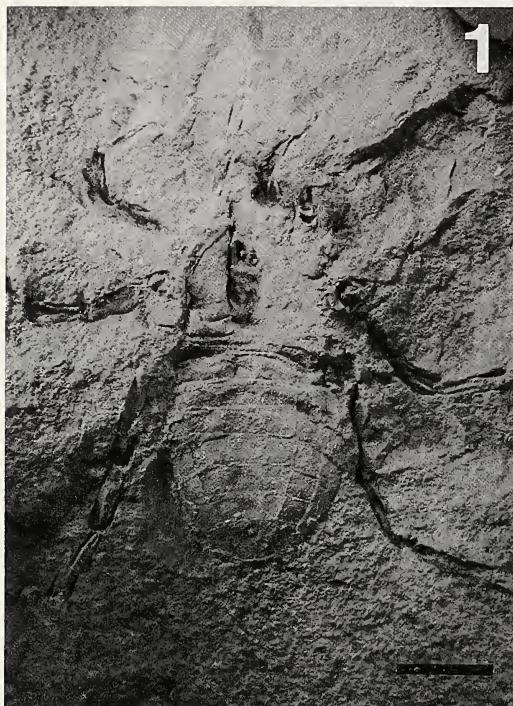
Figures 1, 2.—The holotype of *Lissomartus schucherti* (Petrunkevitch 1913) (YPM 169). From the Pennsylvanian (Westphalian D) of Mazon Creek, Illinois, USA. 1, Part showing dorsal surface; 2, Counterpart showing ventral surface. Scale: 5 mm.
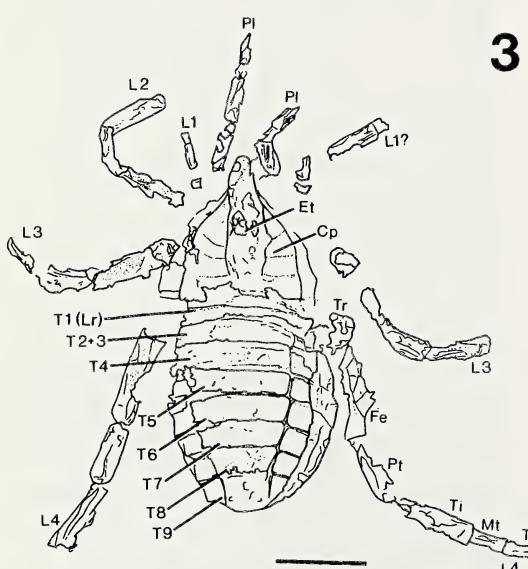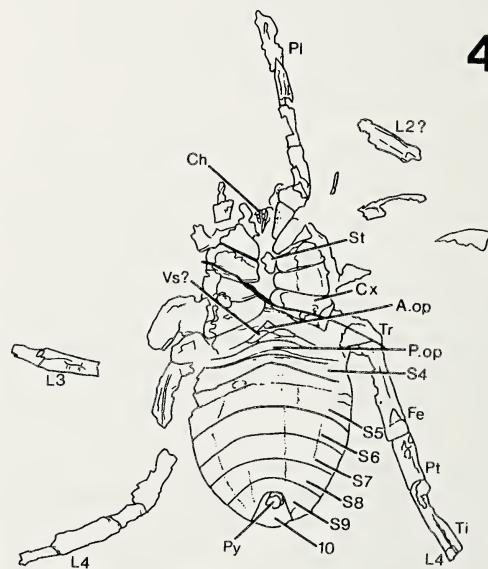
Figures 3, 4.—Interpretative drawing of the specimen shown in Figures 1 and 2. 3, Dorsal surface; 4, Ventral surface. Cp = carapace, Et = eye tubercle, T = tergite with number, Lr = locking ridge, S = sternite with number, A. op = anterior operculum, P. op = posterior operculum, Vs? = ventral sacs?, Py= pygidium, Ch = chelicerae, L = walking leg with number, Pl= pedipalp, Cx = coxae, Tr = trochanter, Fe = femur, Pa = patella, Ti = tibia, Mt = metatarsus, Ts = tarsus, St = sternum. Scale: 5 mm.
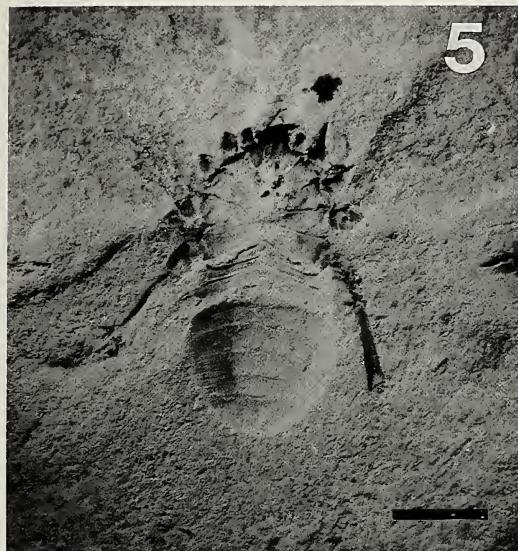
Figure 5.—The holotype of *Lissomartus carbonarius* (Petrunkevitch 1913) (USNM 37978). From the Pennsylvanian of Mazon Creek, Illinois, USA. Ventral surface only. Scale: 5 mm.

Figure 6.—Interpretative drawing of the specimen shown in Figure 5. Abbreviations as in Figures 3 and 4. Scale: 5 mm.

gous with structures seen in some Recent arachnids called ventral sacs whose function is obscure (Dunlop 1994), rather than a genital organ as Petrunkevitch (1949) suggested. However, it is worth noting that male amblypygids have a pair of gonopodi in this position associated with the genitalia (W. Shear, pers. comm.). The presence of a structure on the anterior operculum raises some doubts about the interpretation of the segmentation in this animal, but there is no visible segment in front of the anterior operculum and the overall segmentation pattern favors interpreting these structures as belonging to the anterior operculum. Whether they are ventral sacs or genitalia is impossible to determine, but since the genitalia of many Recent tetrapulmonates are concealed beneath the anterior operculum I favor their interpretation as ventral sacs.

Both specimens show a distinct deepening of the posterior opisthosoma posteriorly from the middle of sternite 5 (Figs. 2, 4–6). This could give the animal a relatively flat, narrow anterior opisthosoma with a deeper, bowl-like posterior opisthosoma (Fig. 7) in lateral view. The division between the ninth sternite and the tenth segment (not divided into a tergite and sternite) is present but poorly defined. Segment 10 surrounds a two-segmented pygidium. This structure is therefore not an anal operculum as interpreted by Petrunkevitch (1949).

The reconstruction of *Lissomartus schucherti* (Fig. 7) is based on YPM 169, with USNM 37978 (*L. carbonarius*) being used primarily for the coxosternal region. The claws and distribution of setae are hypothetical and based on the well-preserved Devonian trigonotarbids (e. g., Shear et al. 1987) and comparisons with Recent arachnids. The *Lissomartus* species are relatively large trigonotarbids and can be visualized as either ambushing or running down small arthropods on the floor of the coal forests.

SYSTEMATIC PALEONTOLOGY

Order Trigonotarbida Petrunkevitch 1949
Family Lissomartidae new family

Type and only known genus.—*Lissomartus* Petrunkevitch, 1949.

Diagnosis.—Trigonotarbids with a medially raised carapace bearing a pair of eyes on a median tubercle. Carapace relatively smooth, but with slight lateral lobation and medial tuberculation. Opisthosoma smooth with tergite 1 present as a locking ridge, tergites 2 + 3 fused and tergite 9 divided into median and lateral tergites.

Sternite 5 large, with the opisthosoma deepening posteriorly.

Discussion. — *Lissomartus* does not show the deep carapace lobation and heavily tuberculated dorsal surface which characterizes trigonotarbids such as *Aphantomartus* (e. g., Pocock 1911; Petrunkevitch 1953; Selden & Romano 1983). On these grounds I reject Petrunkevitch's (1949) placement of *Lissomartus* in the family Aphantomartidae (his Trigonomartidae).

Lissomartus is clearly related to *Trigonotarbus* (e. g., Pocock 1911; Petrunkevitch 1949) on account of its overall carapace shape and lack of strong tuberculation. However, *Lissomartus* can be differentiated from *Trigonotarbus* by its carapace ornamentation and opisthosomal segmentation. Specifically, *Lissomartus* shows fused tergites 2 + 3, a divided tergite 9 and unfused (barely) sternite 9 and segment 10 whereas *Trigonotarbus* has an unfused 2 + 3, an undivided tergite 9 and sternite 9 fused to segment 10 (unpubl. obs.). On these grounds I also reject Petrunkevitch's (1913) placement of *Lissomartus* in the Trigonotarbidae. Since *Lissomartus* cannot be placed in any existing family I am creating a new, monotypic family, Lissomartidae, to accommodate the genus. This family is known only from the Westphalian D of Mazon Creek.

Opisthosomal segmentation and ornamentation patterns appear to be useful characters, visible in most specimens, on which to base higher taxa in trigonotarbids. The Lissomartidae are clearly related to *T. johnsoni* in terms of their carapace shape and opisthosomal smoothness.

Eophrynidae and Aphantomartidae are probably sister groups, sharing a deeply lobed carapace and a heavily tuberculated dorsal surface. Lissomartidae may represent the plesiomorphic sister group of Eophrynidae + Aphantomartidae (with Trigonotarbidae perhaps the sister group to all three) since they do not have the, presumably derived, heavy tuberculation, but share with Eophrynidae + Aphantomartidae a division of tergite 9 (perhaps not fully complete in *Lissomartus*). There is also the slight lobation of the carapace, reminiscent of that in aphantomartids and eophrynids, and the drawing out of the anterior carapace of *Lissomartus*, similar to the pointed anterior spine of eophrynids.

Genus *Lissomartus* Petrunkevitch 1949

Type species. — *Lissomartus schucherti* (Petrunkevitch 1913).

Included species. — *L. schucherti, L. carbonarius*.

Diagnosis. — As for the family.

Lissomartus schucherti (Petrunkevitch 1913)
Figs. 1–4, 7

Trigonotarbus schucherti Petrunkevitch 1913: 106, 107, figs. 63, 64, Pl. 10, figs. 53, 54.
Lissomartus schucherti (Petrunkevitch). Petrunkevitch 1949: 257.
Lissomartus schucherti (Petrunkevitch). Petrunkevitch 1953: 94.
Lissomartus schucherti (Petrunkevitch). Petrunkevitch 1955: 113, fig. 80 (2a, b).

Type. — Holotype and only known specimen YPM (169), part and counterpart. From the Pennsylvanian (Westphalian D) of Mazon Creek, Illinois.

Diagnosis. — Lissomartids with a raised, bilobed structure of the anterior operculum. Ventrally, anterior sclerites not pointed on the midline.

Description. — Holotype 19.0 mm long; carapace 7.9 mm long, basal width 6.5 mm. Opisthosoma 11.1 mm long with maximum width 9.0 mm. Carapace relatively flat, subtriangular, drawn anteriorly into a long, blunt point. Carapace with medial raised area bearing a pair of eyes on a tubercle, 3.0 mm from the front of the carapace. Slight raised nodes either side of, and posterior to, the eye tubercle, otherwise carapace smooth, but slightly lobed either side of the raised median region.

Sternum present, but slightly displaced and not distinct in the fossil. Coxae subtriangular, becoming progressively larger posteriorly. Trochanters approximately as long as wide. Chelicerae present, but indistinct. Other appendages relatively long and slender with a slight granular texture to the cuticle. Pedipalp shows an oblique articulation to the trochanter–femur joint. Podomere lengths (in mm): Palp: Fe 2.9, Pa 2.7, Ti 2.0, Ts 2.9. Leg 1: Ti? 3.7. Leg 2: Fe 4.0, Pa 2.8, Ti 3.7. Leg 3: Fe 3.8, Pa 2.9, Ti 3.7. Leg 4: Fe 5.7, Pa 3.4, Ti 4.1, Mt 1.9, Ts 2.1 mm (abbreviations as in Figs. 3, 4).

Prosoma and opisthosoma slightly disarticulated in this fossil. Opisthosoma rounded, left hand margin being absent and the right hand tergites being obscured along their lateral margins by poorly defined, superimposed sternites. With the exception of tergite 1, tergites divided into median and lateral plates, median plates becoming narrower posteriorly. Division of tergite
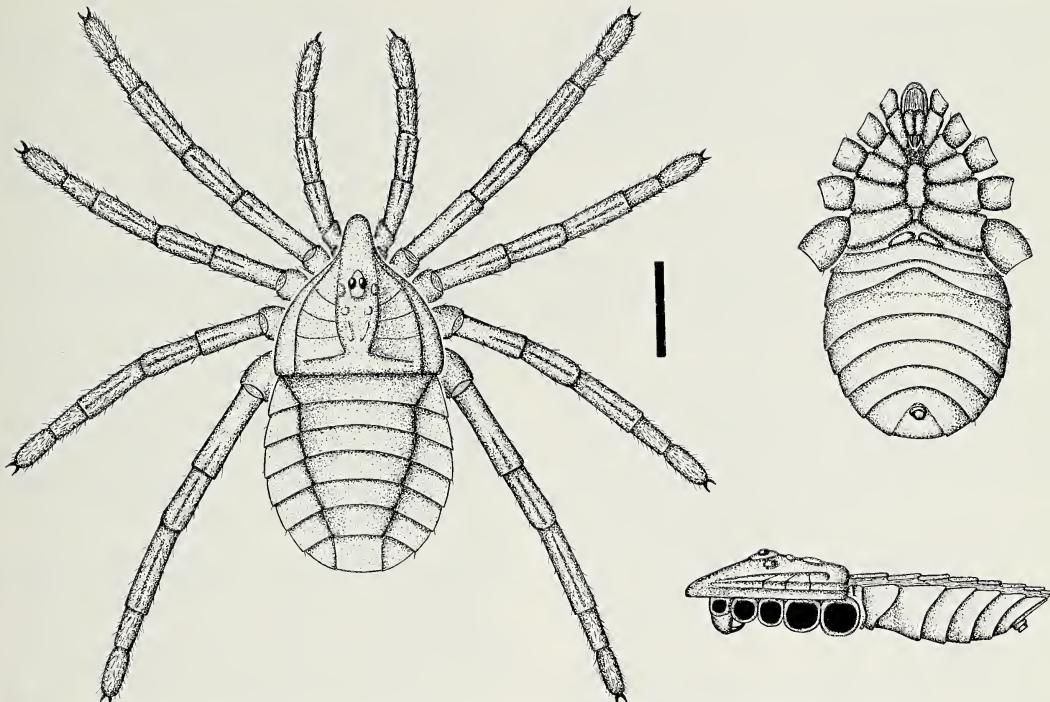
Figure 7.—Reconstruction of *Lissomartus schucherti* in dorsal, ventral and lateral view. Scale: 5 mm.

9 into median and lateral plates weaker than in the preceding tergites. Tergite lengths (in mm): 1: 0.7, 2 +3: 1.2, 4: 1.5, 5: 1.2, 6: 1.5, 7: 1.4, 8: 1.4, 9: 2.2.

Ventrally, anterior sclerites are abbreviated, but are followed by large sternite 5. Anterior operculum bears a raised, bilobed structure on posterior margin. Sternite 5 bears a transverse division (not a segmental division) demarcating a deepening of the opisthosoma posterior to the division. Faint longitudinal folds on the ventral opisthosoma. Ventral sclerites lengths (in mm): anterior operculum: 0.7, posterior operculum: 1.2, sternite 4: 0.4, 5: 2.4, 6: 1.5, 7: 1.3, 8: 1.0, 9: 0.9. Pygidium diameter 0.9 mm.

Lissomartus carbonarius (Petrunkevitch 1913)
Figs. 5, 6

Trigonotarbus carbonarius Petrunkevitch 1913: 107, 8, fig. 65, Pl. 10, fig. 55.
Lissomartus carbonarius (Petrunkevitch). Petrunkevitch 1949: 257.
Lissomartus carbonarius (Petrunkevitch). Petrunkevitch 1953: 94.

Type.—Holotype and only known specimen, USNM 37978, one piece. From the Pennsylvanian (Westphalian D) of Mazon Creek, Illinois.

Diagnosis.—Lissomartids with no raised, bilobed structure on the anterior operculum. Ventrally, anterior sclerites pointed anteriorly on the midline.

Description.—Holotype 16.3 mm long; ventral opisthosoma 9.7 mm long maximum width 7.2 mm. Coxo-sternal region well preserved and shows a sternum, bluntly pointed at either end. Leg 4 coxae attach posterior to sternum, leg coxae 2 and 3 slot into recesses in sternum and leg coxae 1 attach anterior to sternum. Chelicerae present and wedge-shaped in ventral view and with the palpal coxae either side of them they define a small preoral cavity. Femur of leg 4 present and 5.2 mm long. Additional limbs absent.

The prosoma and opisthosoma are slightly disarticulated in this fossil. Anterior segmentation of the opisthosoma clearly shows the abbreviated anterior sclerites pointed anteriorly on the midline and the large 5th sternite behind them. Lengths (in mm): anterior operculum: 0.4, posterior operculum: 0.7, sternite 4: 0.9, 5: 2.1, 6: 1.5, 7: 1.2. Bilobed structure, as in the anterior region of YPM 169, absent, but the deepening of the opisthosoma marked by a transverse division of sternite 5 more pronounced than in

YPM 169. Sternites posterior to this become increasingly poorly defined. Lateral and posterior margins of opisthosoma presumed absent since the pygidium cannot be seen. Lateral margins of the opisthosoma show evidence of folding or wrinkling of the cuticle.

Remarks.—*Lissomartus schucherti* and *Lissomartus carbonarius* are very similar fossils and there is a strong possibility that they are synonymous. In this case *L. carbonarius* would be referred to *L. schucherti* (the first of the two species mentioned by Petrunkevitch (1913)). The minor differences between these fossils could be the result of sexual dimorphism and/or ontogeny, as was suggested by Dunlop (1994) for the trigonotarbid *Pleophrynus verrucosa*. Differences in the anterior opisthosomal (genital) region are recorded within species of Amblypygi and Uropygi (W. Shear, pers. comm.) and there could be a 'straightening' of the anterior sclerites between *L. carbonarius* and *L. schucherti* due to sexual maturation.

However, since there are real morphological differences between the two monotypic species (the lack of a raised bilobed structure and the shape of the anterior ventral sclerites in the smaller *L. carbonarius*) I prefer to retain the species distinction with the reservations noted above; the dimorphic interpretation of *Pleophrynus* above was based on a wide range of specimens. Possibly, future finds of *Lissomartus* will give a clearer picture of intraspecific variation and clarify the position of these species.

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RESEARCH NOTES

A NEW SYNONYM IN THE GENUS *META* (ARANEAE, TETRAGNATHIDAE)

The orb-weaving spider *Meta menardii* (Latreille 1804) has been treated in the past as occupying much of the holarctic region (Bonnet 1957; Roewer 1942; Levi 1980). Recently, however, Marusik & Koponen (1992) concluded that three allopatric species are involved, namely, *M. menardii* in Europe, *M. manchurica* Marusik & Koponen 1992 in the Russian Far East, and *M. americana* Marusik & Koponen 1992 in eastern North America. A fourth related species, *M. japonica* Tanikawa 1993, was subsequently described. My purpose here is to show that there is an available name older than *americana* for the eastern North American species.

Gertsch (1933) described a species of cave spider from Indiana, proposing for it the new genus *Auchicybaeus* and placing it in the family Agelenidae. Soon recognizing his error regarding the generic and familial placement, he synonymized the name *Auchicybaeus* under *Meta*. He also synonymized the specific name *ovalis* under *menardii* (Gertsch & Ivie 1936). Bonnet (1957) recorded the synonymy, but Roewer (1942) and Levi (1980) did not.

I have examined Gertsch's type specimen and have found it to match specimens of the eastern North American species formerly known as *M. menardii* and lately described as *M. americana*. The size, color pattern, cheliceral dentition, eye relations, leg trichobothria, and details of the epigynum and spermathecae of the type lead me to conclude that *ovalis* and *americana* represent a single species. The older name must be used, as formalized below.

Meta ovalis (Gertsch)

Meta menardi: Emerton 1875:129 (part); Gertsch & Ivie 1936:20; Bonnet 1957:2787 (-*i*) (part); Levi 1980: 42, figs. 112–127, map 5; Platnick 1993:376 (-*i*) (part). Not *menardii* Latreille 1804.

Auchicybaeus ovalis Gertsch 1933:11, fig. 15. Holotype female from Marengo Spring Cave, Crawford County, Indiana, 20 October 1911 (Arthur W. Henn), deposited in the American Museum of Natural History, New York. Examined.

Meta americana Marusik & Koponen 1992:138, figs. 1–4, 14. Holotype male from northeast of Jamison, Pennsylvania, June 1944 (W. Ivie), deposited in the American Museum of Natural History, New York, not examined. Male and female paratypes from Eganville, Ontario, 12 June 1972 (S. Peck), deposited in the Canadian National Collection of Insects and Arachnids, Ottawa, Ontario, examined. NEW SYNONYM.

Note: Platnick (1993:376) first used the combination *Meta ovalis* (Gertsch 1933).

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Charles D. Dondale: Centre for Land and Biological Resources Research, Agriculture and Agri-Food Canada, Ottawa, Ontario K1A 0C6, Canada.

THE NEW SPECIES *PURUMITRA AUSTRALIENSIS* (ARANEAE, ULOBORIDAE) WITH NOTES ON ITS NATURAL HISTORY

The genus *Purumitra* Lehtinen 1967 was previously known only from specimens of *Purumitra grammicus* (Simon 1893) collected on the Phillipine island of Luzon and the Caroline island of Ponape (Opell 1979). This paper describes a second species of *Purumitra* that is found on continental islands of the Great Barrier Reef located off the east coast of Queensland, Australia. For nomenclatural purposes, B. D. Opell is designated the author of this new species' name.

We thank the Queensland Department of Environment and Heritage for permission to work on the islands and transportation to some of them. T. W. Schoener thanks the University of Queensland and Professor J. Kikkawa for arranging a visiting professorship, and the John Simon Guggenheim Foundation for the fellowship supporting this research. Robert Bennet made useful comments on the manuscript.

Purumitra australiensi new species
Figs. 1–5, Tables 1, 2

Types.—Female holotype and paratype from Pelican Island (nr. Brampton Island), 30 September 1992 (T. Schoener, S. Keen); male paratype from Cow Island (near Whitsunday Island), 17 October 1992 (T. Schoener, S. Keen); in Queensland Museum (see Fig. 1). The epithet of this species is an adjective derived from its known distribution.

Diagnosis.—*Purumitra australiensis* is similar to *P. grammicus* in size, coloration, and general appearance (Figs. 2, 3; fig. 159 in Opell 1979). Female *P. grammicus* has an epigynum with a pair of lateral crypts and a median crypt that is subdivided by sclerotized ridges into a pair of anterior and a pair of posterior atria (fig. 160 in Opell 1979). In contrast, the epigynum of *P. australiensis* has a pair of lateral crypts and a large, undivided median crypt (Fig. 5). The male palpus of *P. grammicus* has a median apophysis bulb (MAB) whose central depression is completely divided by a narrow sclerotized ridge into a small region that is adjacent to the median apophysis spur (MAS) and a larger region near the MAB's dorsal surface (fig. 157 in Opell 1979). The width of this species' concave median

apophysis spur (MAS) is 0.7× its length. In contrast, the MAB of a palpus of *P. australiensis* (Fig. 4) has a central depression incompletely divided by a short sclerotized ridge into a large region ventral to the MAS (above the MAS in Fig. 4) and a small region near the base of the MAB. In *P. australiensis* the width of the concave MAS is only 0.4× its length.

Description.—Table 1 gives measurements of male and female specimens. As shown in Fig. 2, the carapace of a female is dark gray with median
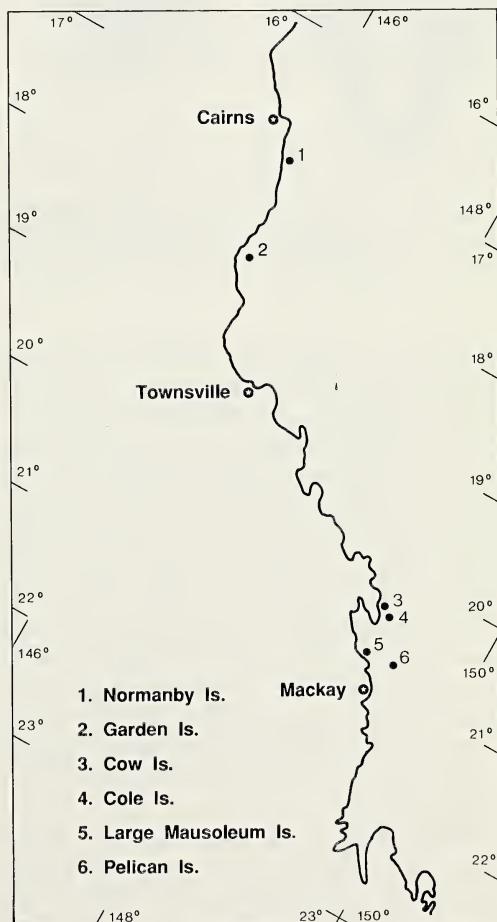
Figure 1.—The east coast of Queensland, Australia, showing the location of the islands on which specimens of **Purumitra australiensis** new species were collected.
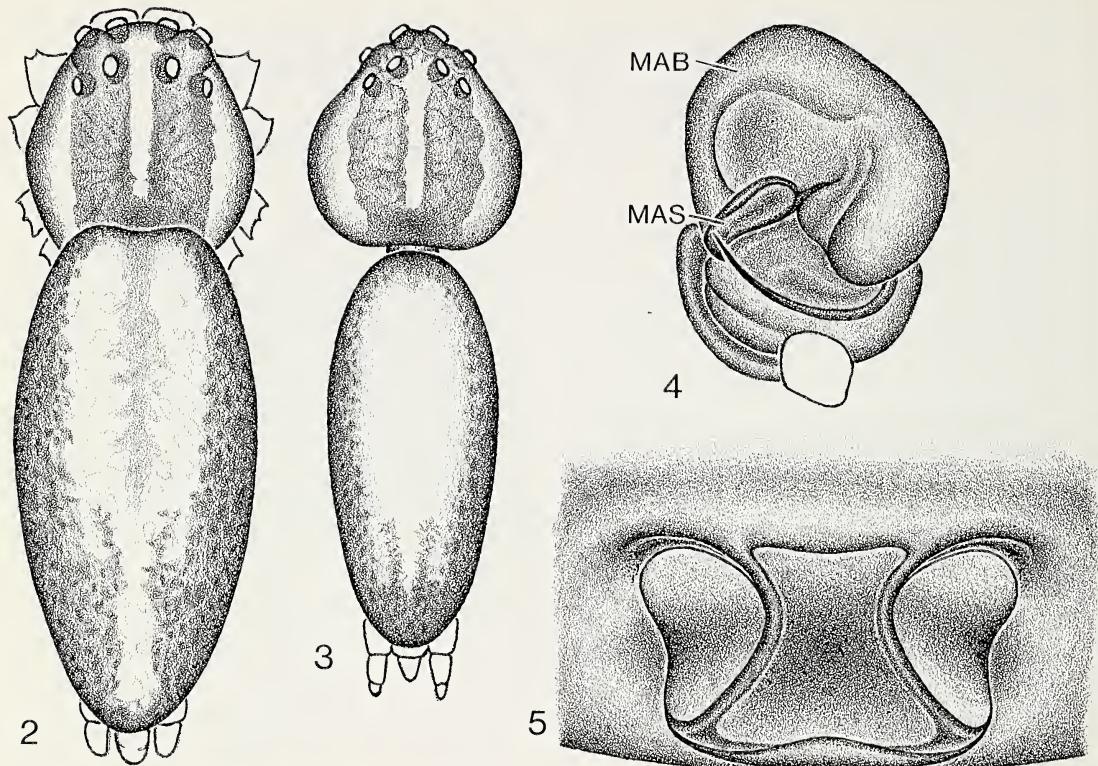
Figures 2–5.—*Purumitra australiensis* new species. 2, dorsal view of female holotype; 3, dorsal view of male paratype; 4, retrolateral view of left palpal genital bulb of male paratype (MAB = median apophysis bulb, MAS = median apophysis spur); 5, ventral view of epigynum of female holotype.

and lateral tan stripes. The carapace also has a narrow, dark gray border not easily seen in dorsal view. Sternum dark gray. Chelicerae with a pair of narrow, black, dorso-ventral stripes. First legs gray with dorsal white stripe extending full length of femur, proximal white ring on metatarsus, and faint tan ring at center of tibia. Abdomen in dorsal view (Fig. 2) white with mottled gray sides; in lateral view mottled gray with a broad white stripe extending nearly its full length; in ventral view dark gray with a narrow, broken, median tan stripe and a pair of narrow, paraxial tan stripes. Male coloration (Fig. 3) similar to that of female except that the sternum has a light gray center and a dark margin and the first tibia is uniformly gray.

Natural history.—All specimens were collected from horizontal orb webs among understory/edge vegetation (including ferns) within forest very near the shoreline. Webs were located near the ground; all had a stabilimentum (Table 2). Webs of juveniles were nearer the ground than those of mature females and were about as likely

Table 1.—Measurements in mm of female holotype and male paratype of *Purumitra australiensis* new species.

	Female	Male
Total length	2.52	2.28
Carapace length	0.84	0.84
Maximum carapace width	0.72	0.72
Clypeus height	0.03	0.01
AME, ALE diameter	0.08, 0.05	0.08, 0.05
PME, PLE diameter	0.08, 0.06	0.06, 0.06
AME, PME separation	0.08, 0.14	0.08, 0.11
Sternum length	0.56	0.48
Maximum sternum width	0.44	0.36
Coxa-trochanter I	0.36, 0.36	0.32, 0.28
Femur I, IV	1.44, 0.96	1.32, 0.76
Patella I, IV	0.36, 0.28	0.32, 0.24
Tibia I, IV	1.24, 0.80	1.20, 0.64
Metatarsus I, IV	1.24, 0.70	1.12, 0.56
Tarsus I, IV	0.64, 0.56	0.56, 0.44
Calamistrum length	0.38	—
Abdomen length	2.00	1.60
Maximum abdomen width	0.96	0.64
Cribellum width	0.20	—

Table 2.—Web placement and web features of *Purumitra australiensis* new species.

	Juveniles	Adult females
Height above ground in cm (mean ± 1 SD, *n*)	20.3 ± 4.8, 5	27.3 ± 7.6, 4
Stabilimentum type: No. with linear/ No. with circular	3 / 2	1 / 4

to have linear as circular stabilimenta. Webs constructed by adult females usually had circular stabilimenta.

Distribution.—Mature specimens were collected on the following continental islands from September 30–November 28 1992 (Fig. 1): Large Mausoleum (Newry Island Group, near Cape Hillsborough), Pelican Island (near Brampton Island), Cole and Cow Islands (both in Whitsunday Island area), Normanby Island (Frankland Group, south of Cairns), Garden Island (south of Family Islands).

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Brent D. Opell: Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA.

Thomas W. Schoener and **Susan L. Keen:** Section of Evolution and Ecology, Division of Biological Sciences, Storer Hall, University of California at Davis, Davis, California 95616 USA.

Valerie T. Davies: Queensland Museum, P.O. Box 3300, South Brisbane, Queensland 4101, Australia.

A GYNANDROMORPHIC *SCHIZOCOSA* (ARANEAE, LYCOSIDAE)

Individuals in which both sexes are discretely combined are termed gynandromorphs, whereas intersexuality is a condition in which portions of a body are intermediate between the sexes and are not clearly one sex or the other (White 1973; Roberts & Parker 1973). The earliest reference to a spider gynandromorph is given by Blackwall 1867 (cited in Bonnet 1945). Bonnet lists numerous other early citations of gynandromorphs. Roberts & Parker (1973) provide a classification of 14 types of gynandromorphs, which are combinations of lateral and transverse gynandromorphs, although they admit that several of these could never be externally recognized.

Gynandromorphs probably occur in most taxa of animals including birds (Patten 1993), as well as in many insects and arachnids (Hannah-Alava 1960; Cokendolpher & Francke 1983; Brust 1966). They have been studied extensively in *Drosophila* (Wilkins 1993) and as early as the 1920's, gynanders were used as a means of fate mapping cells. Several mutations in *Drosophila* are particularly prone to being gynandromorphic (White 1973). Only slightly more than 50 cases of gynandromorphy and intersexuality have been reported for spiders (Hull 1918; Bonnet 1934; Kaston 1961; Roberts & Parker 1973). It occurs but is perhaps equally rare in scorpions, solpugids and ticks, although reduced sexual dimorphism may make detection more difficult (Cokendolpher & Sissom 1988). Clarke & Rechav (1992) note that gynandromorphs are "widespread" in the Ixodidae, but they do not offer any estimates on the frequency of occurrence.

Kaston (1961), in his summary of the spider gynandromorphs known to that point, suggested that gynandromorphy in spiders is "exceedingly rare." Palmgren (1979) calculated a rough estimate of the frequency of gynandromorphism based on 69,970 adult spiders from his own collection and from the Zoological Museum of the Helsinki University Collection. He described four gynandromorphs and suggested that the phenomenon occurs about once per 17,000 normal spiders. One of the specimens described by Palmgren was from the genus *Oedothorax*. Holm (1941) noted that a disproportionate number of gynandromorphic specimens are in this genus.

The causes of gynandromorphy have been investigated for a variety of groups (but not spiders) and generally involve the nondisjunction in the X chromosomes early in development (White 1973). For example, in a species of tick studied by Homsher & Yunker (1981), the male tissue had the number of chromosomes typical for males $(22 + X)$ while the chromosomes in the female tissue were consistent with that of a normal female of that species $(22 + XX)$. Presumably the mechanism of formation of gynandromorphs in spiders is the same as in these other groups; however, there have been no published studies of the karyotype of gynandromorphic spiders (White 1973). Kaston (1961) suggested that the phenomenon of gynandromorphy would be less frequent in spiders than insects (particularly *Drosophila*) because of the chromosomal system found in spiders. In many spiders the males are "X1X20" or "X1X2X30," and females "X1X1X2X2" or "X1X1X2X2X3X3" where females have two, three, or more chromosomes than males (White 1973; Hackman 1948; Wise 1983). Kaston suggested that the creation of a gynandromorph from a chromosomal female zygote would involve the loss of 2–3 chromosomes, rather than just one as in *Drosophila* and would thus be quite a bit less frequent in most spiders than in *Drosophila*.

Although some behaviors in a few gynandromorphs have been noted (e. g., *Coelotes atropos* produced an egg sac (Kaston 1961)), the most extensive behavioral description is that of the lycosid *Alopecosa pulverulenta* provided by Gack & von Helversen (1976). These authors described the individual as a "lateral gynandromorph" in which the left side was male and the right side female, except for the right palp which was described as intersexual. The ventral opisthosoma contained male sexual organs. When the gynandromorph was placed with a normal male spider of the same species, the male did not exhibit courtship behavior. This perhaps suggests that the gynander lacked pheromones that are often produced by female lycosids that elicit courtship in males. The gynander never mated with the male. However, the gynandromorph spider built an egg case that contained only a gelatinous fluid and was *not* carried on the spinnerets. When placed with a normal female of the same species, the gynandromorph showed courtship behavior typical of the males of its species, mounted and inserted the male palp in a manner
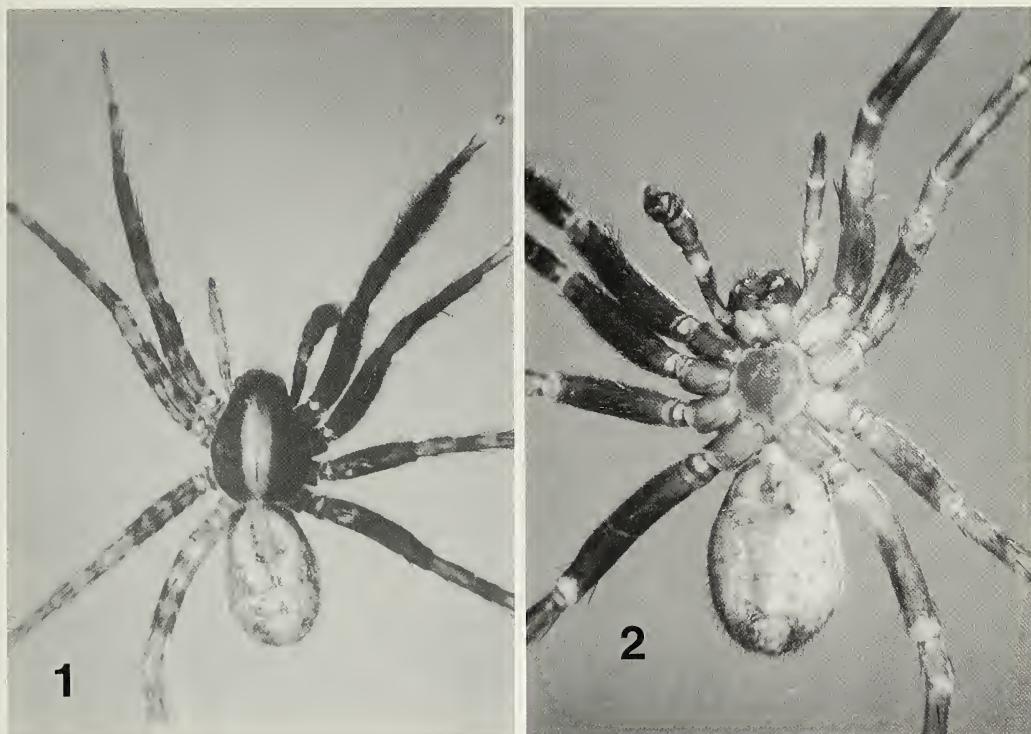
Figures 1, 2.—Gynandromorphic *Schizocosa ocreata* from Hue, Hocking County, Ohio. 1, Dorsal view of gynandromorphic *Schizocosa ocreata*. Right side of individual shows male palp; left side shows female palp; 2, Ventral view showing differences in coloration of legs, sternum and venter.

also typical of the species. It made no attempt to insert the other (intersexual) palp. Copulation was short and involved only one insertion. (The species typically shows several insertions). The gynandromorph mated with a second female. The authors do not report if either of the females laid an egg case following this mating.

The present report provides a description of a gynandromorphic *Schizocosa ocreata* (Hentz) discovered in the summer of 1993 and a rough estimate of the frequency of gynandromorphism in this genus. This is the first report of a gynandromorph in the genus *Schizocosa*, although occurrences have been reported in other lycosids (Exline 1938; Holm 1941; Kaston 1961; Mackie 1969; Gack & von Helversen 1976).

The specimen of *Schizocosa* described here was from Ohio, Hocking County, Hue. It was collected in a house on 25 June 1993 by Lawrence M. King III (a former undergraduate student of Jerome Rovner) who suspected that it was a gynandromorph. The spider was given to J. Rovner, who noted that it walked in a manner typical of male *S. ocreata* by extending and tapping the front legs (pers. comm.).

Description.—By using the classification suggested by Roberts & Parker (1973), I would suspect that this specimen is a regular Type 2 gynandromorph, although like many gynandromorphs, it is not perfectly symmetrical (Figs. 1, 2). The left side of the spider is female, its right side male. The total length is 7.8 mm and is within the range for both males and females of this species (Dondale & Redner 1978 report that the size range for males of *S. ocreata* is 5.65–8.3 mm; for females, 7.3–10.4 mm). The carapace length is 3.64 mm, and the carapace width 2.8 mm. The right (♂) side of the carapace is 1.3 mm from edge to the middle; the left (♀) side is 1.5 mm, resulting in a slightly asymmetrical carapace. Likewise, the chelicera on the left side is slightly larger and the fang on this side also is longer. The spinnerets reflect the same pattern: on the left (♀) side, the spinnerets are larger.

The right side of the animal has a fully developed and apparently normal ♂ palp (Fig. 3). There is a stridulatory organ located on the tibio-tarsal joint of this palp. Leg I on the right side has a brush of bristles along the tibia, as is typical for males of this species (Fig. 1). The brush extends
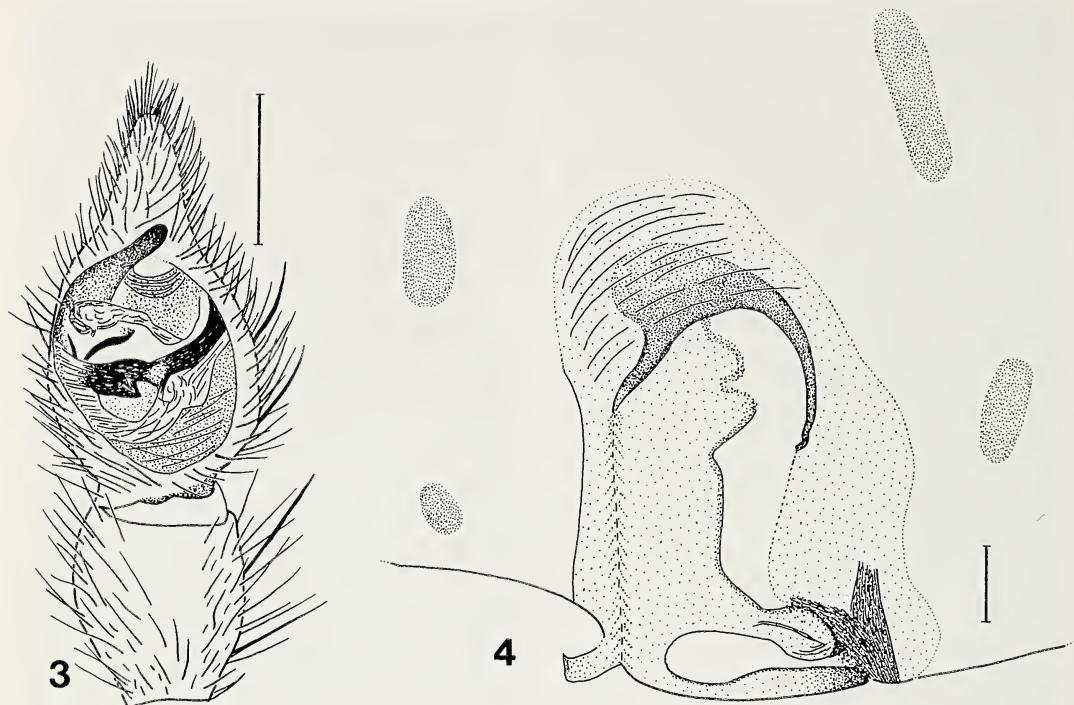
Figures 3, 4.—Gynandromorphic *Schizocosa ocreata*. 3, Ventral aspect of spider's right palp, scale bar = 0.5 mm; 4, Detail of spider's epigynal area, scale bar = 0.1 mm.

to the basitarsus. The left side has a palp resembling that of normal females, and on the opisthosomal venter there is an epigynum that has a single large excavation (Fig. 4). This half of the epigynum looks normal for this species except that the median septum has an irregular border.

The ventral aspect of the animal exhibits two different colorations (Fig. 2). On the spider's right (♂) side, the sternum is darker, although not in a straight line down the sternum. There is a dark band on the right side of the venter of the abdomen, and the pattern of pigmentation on each side of the venter of the abdomen differs. The right side appears mottled, while the left side has distinct dark spots of pigment.

The ventral surface of all four coxae and femora on the right side is black (Fig. 2). On the left (♀) side, the coxae and femora have patches of dark pigmentation but are overall much lighter. In a manner that is atypical for males of *S. ocreata*, the legs on the male side are uniformly dark. Curiously, the tibia of leg II has a rudimentary brush. Legs II–IV on the spider's right side are more similar to a typical male leg I than they are to typical legs II–IV. From a dorsal view, the legs on the left side are annulated, while the legs on

the right are mostly black with some lighter streaks. In most *S. ocreata*, legs II–IV of the males have annulations but are not uniformly dark.

The venter of the abdomen has numerous spots of sclerotization that are more evident on the male side. The dorsum of the abdomen has a heart-mark and the pigmentation on the abdomen is slightly asymmetrical.

Estimation of frequency of gynandromorphs in *Schizocosa*.—My work for the past three years, including much done in collaboration with Gary L. Miller and Patricia R. Miller, provides a rough estimate as to the frequency of this phenomenon in the genus *Schizocosa*. For each of the summers of 1993 and 1994 we have maintained nearly 1000 specimens of *Schizocosa* and other lycosids in the laboratory for behavioral studies. We have also completed a year-long pitfall study, focusing primarily on the lycosids. Thus, we have identified and/or observed behavior in close to 3000 individuals of Lycosidae (mostly *Schizocosa*), and have never encountered a gynandromorph. In earlier studies done at Ohio, I raised or collected nearly an additional 2000 spiders. Thus, an estimate of the frequency of gynandromorphs in this genus is that one may occur not more fre-

quently than once every several thousand spiders.

The specimen is currently housed in the teaching collection of Jerome Rovner at Ohio University.

ACKNOWLEDGMENTS

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Gail E. Stratton[1]:   Dept. of Biology, Albion College, Albion, Michigan 49224 USA

[1]Current address: Rhodes College, 2000 N. Parkway, Memphis, Tennessee 38112-1690.

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Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P. N. Witt & J. S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33, dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28, *A-us x-us,* holotype male; 33, 34, *A-us y-us,* male. Scale = 1.0 mm.

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Cover illustration: Scanning electron microscope photograph of the abdomen of a mature female *Philoponella vicina* (Uloboridae). Photograph by Flory Pereira and William G. Eberhard.

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THE WEB-SPIDER COMMUNITY OF SOYBEAN AGROECOSYSTEMS IN SOUTHWESTERN OHIO

Ann L. Rypstra and **Paul E. Carter**: Department of Zoology, Miami University; Hamilton, Ohio 45011 and Oxford, Ohio 45056 USA

ABSTRACT. We documented the web-spider community in a soybean agroecosystem over the entire growing season in 1990 and 1991 and over the period of peak spider abundance in August of 1993. Simultaneously a number of vegetational parameters were quantified in order to determine the extent to which the spider abundance was correlated with characteristics of the plant community. Web-spider abundance was higher in 1991 than in 1990 or 1993 and lower in 1993 than the other two years. The composition of the community in terms of web-types also differed among years with sheet webs (Linyphiidae, Agelenidae) being much more abundant in 1991 and orb webs (Araneidae) more abundant in 1990. In 1991, spider abundance was correlated with specific vegetation characteristics which suggests that the availability of habitat was important to spider colonization and establishment in that year. However, in 1990 spider abundance was not correlated with any of the vegetation characteristics we measured. The late season spider density was positively correlated with weed biomass and the damage inflicted on the soybean leaves by herbivores was negatively correlated with the number of web-spiders across the three years. These data suggest that the web-spider community responds to some aspects of the plant community and that they have the potential to impact plant production by reducing the action of herbivores.

Spiders are common generalist predators on arthropods in many agricultural systems. In spite of this fact, little data exist on their activities in these systems (Riechert & Lockley 1984; Nyffeler & Benz 1987; Young & Edwards 1990; Wise 1993). Because spiders are generalist predators and most efforts to implement biological control have focused on predator or parasitoid interactions to reduce the impact of specific pests, spiders have not been considered seriously (Riechert & Lockley 1984; Nyffeler & Benz 1987). In addition, spiders have relatively long generation times and agricultural habitats are frequently disturbed by activities such as plowing and planting, which means that a large proportion of the spider community has to be re-established each season (Riechert & Lockley 1984; Young & Edwards 1990). It is not yet clear how predictable the spider community is from year to year and what factors might influence it most directly.

Plants are important modifiers of the microclimate for arthropods, specifically by moderating temperature and humidity extremes and by providing a more complex three-dimensional habitat (Cloudsley-Thompson 1962). The changes plants cause are dramatic in strongly seasonally systems like agricultural fields where areas are specifically managed to proceed from no vegetation to a continuous cover of vegetation in a few months. As crop plants develop, the fields gradually become more hospitable to colonization by spiders and other arthropods because the plants provide structure, shade and help maintain moisture. Web-building spiders are particularly dependent on vegetation to provide suitable web-attachment sites (Greenstone 1984; Rypstra 1986; Uetz 1991). Data suggest that spider colonization via aerial dispersal peaks early in the growing season (Bishop 1990; Bishop & Riechert 1990) so developmental rate and spacing pattern of crop plants should influence the establishment of the spider community in agroecosystems (Ferguson et al. 1984; Stinner & House 1990).

In the United States, 262 species of spiders have been found in soybean (*Glycine max* (L.) Merrill) fields (Young & Edwards 1990). In a given area, the number of spider species is likely to be less than that number, but soybeans typically contain one of the most diverse communities seen in any agricultural crop (LeSar & Unzicker 1978; Young & Edwards 1990). Culin & Rust (1980) reported that the foliage community of spiders in soybeans responded across the season to habitat space, a measure of plant development, whereas the ground dwelling spider community changed less over the season. Further evidence of the response of spiders to the soybean vegetation is apparent in comparisons among different cropping systems. Typically more

foliage-dwelling spiders have been found in fields where the plants were closer together and the cover more continuous than in other fields (Sprenkel et al. 1979; McPherson et al. 1982; Ferguson et al. 1984).

In this study we focused on specific aspects of how the plant abundance and structure might be related to the web-spider community that developed in soybeans. We attempted to determine how closely the spiders tracked vegetation development in this system by monitoring both spiders and plants weekly for two full seasons. In a third season, we collected data only at the time of peak web-spider and vegetational abundance in order to assess how predictable the web-spider guild composition was from year to year and to determine which vegetational characteristics might be most closely tied to spider abundance across years.

METHODS

Study area.—The study was conducted in soybean monoculture plots located at the Miami University Ecology Research Center, three miles north of Oxford, Butler County, Ohio, USA (Kemp & Barrett 1989). Each plot measured 60 × 70 m and contained 82 rows of soybeans planted in an east-west direction. Experimental plots were bordered on all sides by a 15 m mowed grass strip. Four plots were randomly selected from an array of 12 in 1990 and three plots were selected from that array in 1991 and 1993.

Herbicides were applied to all plots in all years. The pre-emergence herbicides, Lorox Plus® (linuron plus chlorimuron; 0.51 kg active ingredient/hectare) and Dual 8E® (metolachlor; 1.4 kg active ingredients/hectare), were applied to control for broadleaf and grassy weeds, respectively, in all three years. In 1991 and 1993, the post-emergence herbicide, Poast Plus® (sethoxyoim plus dash; 0.28 kg active ingredients/hectare) was applied three weeks after planting to control grassy weeds. All herbicide treatments were applied before we began sampling the plots. No insecticides were applied to the plots in any year.

Plant characteristics.—Vegetation development was monitored weekly in each plot. We measured the height and width of five plants selected by generating random coordinates which determined meter points in a plot each week from three weeks after plant emergence until harvest. In order to obtain a measure of vertical leaf distribution and therefore the availability of possible web attachment points on the soybean

plants, we placed a meter stick through the center of each of the five plants and recorded the height of each leaf touching the stick. Foliage height diversity (H') was then calculated from the leaf height measurements where $H' = -\Sigma p_i \ln p_i$ (p_i = the proportion of the total number of leaves within a 10 cm interval of soybean plant height) (Shannon & Weaver 1949).

Total above ground production was measured just before the soybeans began to senescence (stage R6 as designated by Fehr & Caviness 1977) in all three years. On 7–10 September 1990, 16–20 August 1991 and 1993 four locations were selected randomly within each plot. One row meter of the soybean plants was clipped at the soil surface and collected. In addition the weeds in the area extending to the center point between rows on either side were clipped and collected. Plants were placed in a drying oven at 80 °C for at least seven days and then weighed.

We assessed the cumulative damage inflicted by leaf chewing insects to soybean plants over the season by measuring leaf damage at the end of the season. Two sites in each plot were selected by generating random number coordinates. In 1990 on 10 September, we traced 10 leaflets onto index cards at each site. On 24 August in 1991 and 1993, we traced 12 leaflets at each site. Leaflets areas were then determined to the nearest 0.1 cm² using a calibrated grid.

Spiders.—We monitored the web-spider community in the soybean plots by sampling four 1 m row lengths in each plot each week from the third week after plant emergence (early June) until harvest (late September) in 1990 and 1991 and from mid-season (mid July) to harvest in 1993. Specific row sections to be sampled were determined using different randomly generated coordinates each week. At each site, the plants and soil were visually searched for web-spiders between 0750–1050 h when dew made the webs most visible. Most web-spiders present in the fields were juveniles, which were difficult to identify, especially without collection. Therefore, web-spiders were classified by web type (sheet, orb, or tangle). Sheet-web weavers (Linyphiidae, Agelenidae) build webs that are characterized by a dense horizontal plane of silk frequently with a barrier web consisting of a tangle of silk surrounding the sheet to some degree. Orb-web weavers (Araneidae) consist of a circular plane of silk spirals with supporting spoke strands radiating from the hub. Tangle-web weavers (Theridiidae) build a three-dimensional and somewhat

Table 1.—The soybean growing season was separated into three time periods based on the developmental stage of the plants.

Year	Early	Middle	Late
1990	10 July–23 August	24 August–20 September	21 September–13 October
1991	5 July–5 August	6 August–2 September	3 September–28 September
1993	28 June–24 July	25 July–28 August	29 August–25 September

irregular mesh of strands connecting the vegetation.

Data analysis.—The soybean season in Ohio typically encompasses a four-month period from planting to harvest. The period of study shifted each year due to weather differences and the timing of planting. For ease of comparison relative to the maturity of the plants, we divided each year into early, middle and late month-long time periods (Table 1). For years in which we had data for the entire season, a mean for each plot was generated for each of the three time periods. We then tested for differences between years and season nested in year using a repeated measures analysis of variance. Comparisons of just the late season information across the three years were made using a one-way analysis of variance. The Tukey-Kramer Test was used to make pairwise comparisons among years. Mean spider abundance in the late season was regressed on those vegetation parameters that differed across all three years in an attempt to explain yearly variation in spider abundance. The 1990 and 1991 seasonal data were analyzed separately to dissect

Table 2.—Summary of vegetation data from the soybean fields (Mean ± SD). ANOVA statistics for plant height, width, and H′ are results of repeated measures test for differences among years and season nested in year. Statistics for biomass and leaf damage are from one-way ANOVA.

	1990	1991	1993
Plant height (cm)			
Early	47.1 ± 2.9	41.2 ± 4.6	51.2 ± 3.7
Middle	74.9 ± 2.2	89.7 ± 2.4	92.6 ± 3.2
Late	72.5 ± 1.4	94.0 ± 2.0	95.2 ± 2.1
	year, season (year): $F = 168, 49.8$; $df = 2,6$; $P < 0.05$		
Plant width (cm)			
Early	47.5 ± 3.2	44.7 ± 3.3	42.3 ± 3.1
Middle	69.1 ± 1.7	65.8 ± 2.2	68.0 ± 2.3
Late	41.8 ± 3.1	61.3 ± 4.7	64.7 ± 5.7
	year, season (year): $F = 33.7, 7.9$; $df = 2,6$; $P < 0.05$		
Foliage height diversity (H′)			
Early	1.44 ± 0.05	1.48 ± 0.03	1.54 ± 0.06
Middle	1.87 ± 0.03	1.88 ± 0.04	1.92 ± 0.05
Late	1.27 ± 0.14	1.67 ± 0.10	1.74 ± 0.12
	year, season (year): $F = 16.06, 10.2$; $df = 2,6$; $P < 0.05$		
Soybean biomass (g)			
Late	174 ± 32	356 ± 89	423 ± 97
	year: $F = 32.45$; $df = 2$; $P < 0.05$		
Weed biomass (g)			
Late	503 ± 153	987 ± 102	68 ± 49
	year: $F = 46.13$; $df = 2$; $P < 0.05$		
Leaf damage (%)			
Late	5.9 ± 0.6	2.2 ± 0.4	26.7 ± 4.5
	year $F = 56.56$; $df = 2$; $P < 0.05$		
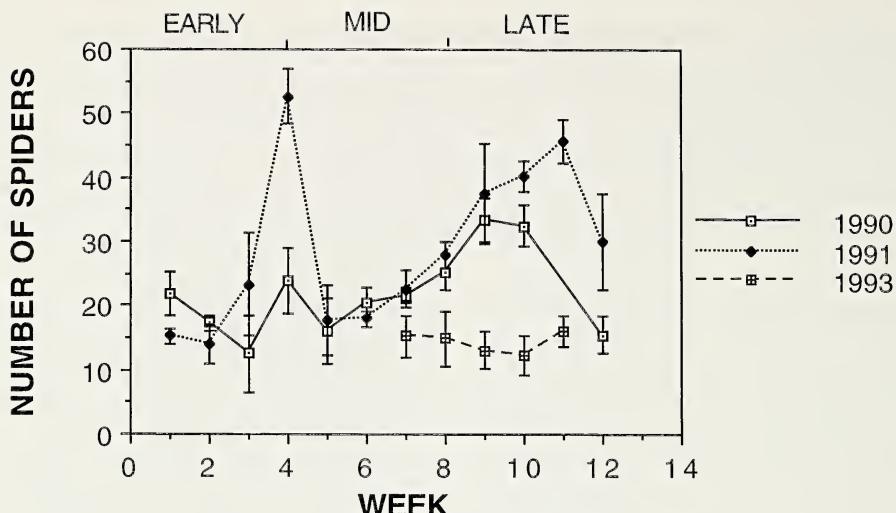
Figure 1.—Spider abundance (per four one-meter row sections) in soybean plots over the entire growing season in 1990 and 1991 and the latter part of the season in 1993 (Mean ± SD).

how closely the spiders tracked the changes in vegetation. Weekly values of the number of spiders were regressed on weekly values for vegetation height, width, and foliage height diversity.

RESULTS

Vegetation.—Soybean plant size differed significantly among years but those differences were only really apparent in the middle and late portions of the season so there was a significant seasonal effect as well (Table 2). Plants were larger and more complex (as measured by foliage height diversity) in 1991 and 1993 than they were in 1990 (Table 2). Likewise, the above ground soybean biomass of one row meter at the peak of lushness (R6) was significantly greater in 1991 and 1993 than it was in 1990 (Table 2). The above ground biomass of weeds surrounding one meter of soybean plants weeds also varied among years (Table 2). The Tukey-Kramer Pairwise Comparisons Test revealed that there was greater weed biomass in 1991 than in 1990 or 1993 and weed biomass was higher in 1990 than it was in 1993 (Table 2). The proportion of each leaflet damaged was also different from year to year (Table 2). Chewing insects damaged the soybean plants much more dramatically in 1993 than in 1990, and plants in both 1990 and 1993 received more damage than in 1991 (Table 2) (Tukey-Kramer Test, $P < 0.05$).

Spiders.—There were significantly more web spiders found in 1991 than in 1990 across the whole season (Fig. 1) (repeated measures of year, season (year): $F = 9.81$, 6.15, $df = 1, 5$, $P < <0.05$). There was considerable overlap in the early and mid-season numbers but the abundances clearly separated by year in the late season (Fig. 1). We did not collect early or mid-season data for 1993, but there were significantly fewer spiders in the late season of that year than in the late season of either of the other two years (Fig. 1) ($F = 60.91$, $df = 2$, $P < 0.05$).

Sheet webs were the most abundant web type in the soybean fields and, at the time of peak spider abundance in the late season, they comprised over 40% of the spiders we observed in all three years (Fig. 2). Sheet webs were significantly more abundant in the 1991 season than they were in 1990 (Table 3). There were no seasonal differences in sheet web abundance in 1990 or 1991 (Table 3). If we compare the late season data from all three years, there were significantly more sheet webs in the fields in 1991 than in the other two years (Table 3) (Tukey-Kramer Test, $P < 0.05$). More than 75% of the sheet-web builders in the plots in all three years belonged to five species (Table 4).

Orb webs were second in abundance to sheet webs in 1990 and 1993 when they comprised more than 25% of the late season community, but they were very uncommon in 1991 (Fig. 2). Unlike sheet-web spinners, the orb-web weavers were significantly more abundant across the season in 1990 than they were in 1991 (Table 3).

Table 3.—Abundances of the three common web types in soybean fields (Mean ± SD). ANOVA statistics are results of repeated measures test for differences between 1990 and 1991, and for season nested in year. Late season data indicated with "*" were significantly different from other years by Tukey-Kramer Pairwise Comparison Test ($P < 0.05$).

	1990	1991	1993
Number of sheet webs			
Early	10.9 ± 6.0	23.0 ± 4.5	---
Middle	11.6 ± 3.1	18.0 ± 3.1	---
Late	11.5 ± 2.7	26.6 ± 3.8*	6.3 ± 4.0
year, season (year): $F = 38.27, 1.7$; $df = 1,5$; $P < 0.05, P > 0.1$			
Number of orb webs			
Early	5.6 ± 1.3	3.7 ± 1.4	---
Middle	5.7 ± 1.4	2.0 ± 0.3	---
Late	11.1 ± 2.2*	3.9 ± 0.5	3.3 ± 1.2
year, season (year): $F = 50.13, 10.39$; $df = 1,5$; $P < 0.05$			
Number of tangle webs			
Early	0.8 ± 1.0	0.7 ± 0.6	---
Middle	1.0 ± 0.5	0.3 ± 0.3	---
Late	2.9 ± 0.7	4.6 ± 0.8	0.9 ± 1.0*
year, season (year): $F = 0.69, 22.21$; $df = 1,5$; $P > 0.1, P < 0.05$			

Additionally there was a significant seasonal increase in the number of orb webs that we were able to find in 1990 (Table 3). In a comparison of late season data of all three years, orb web abundance was significantly higher in 1990 than it was in either of the other two years (Table 3) (Tukey-Kramer Test, $P < 0.05$). Five species comprised better than 75% of the orb-web weavers that we observed in this habitat (Table 4).

Tangle-web weavers were least abundant of the web-spinners, comprising less than 15% of the web-spider community in the soybean fields in the late season of all three years (Fig. 2). There was not a significant difference between the abundance of tangle web weavers in 1990 and 1991 (Table 3). However, the abundance of spiders building tangle webs was significantly greater later in the season than it was in the early or middle portions in those years (Table 3). In a comparison of the late season data on tangle weaver abundance, there were significantly fewer in 1993 than in the other two years of this study (Table 3). Four species of tangle-weavers were collected in all three years (Table 4).

Spiders in relation to vegetation. — Total web-spider abundance across the season was correlated with many of the vegetation parameters in 1991, but was not correlated with any of these parameters in 1990 (Table 5). In 1991, the strongest correlation was between soybean plant width and web-spider abundance. However, foliage height diversity, and plant height were also significantly correlated with spider abundance in that year (Table 5).

Table 4. — List of most common spider species found in the soybean fields categorized by web type.

Sheet-web weavers
  Agelenidae
    Agelenopsis pennsylvanica (C. L. Koch)

  Linyphiidae
    Frontinella pyramitela (Walck.)
    Meioneta micaria (Emerton)
    Tennesseellum formicum (Emerton)
    Microlinyphia pusilla (Sundevall)

Orb-web weavers
  Araneidae
    Argiope aurantia Lucas
    A. trifasciata (Forskal)
    Cyclosa conica (Pallas)
    Neoscona arabesca (Walck.)
    Tetragnatha laboriosa Hentz

Tangle-web weavers
  Theridiidae
    Achaearanea tepidariorum (C. L. Koch)
    Theridion frondeum Hentz
    T. neshamini Levi
    Theridula opulenta (Walck.)
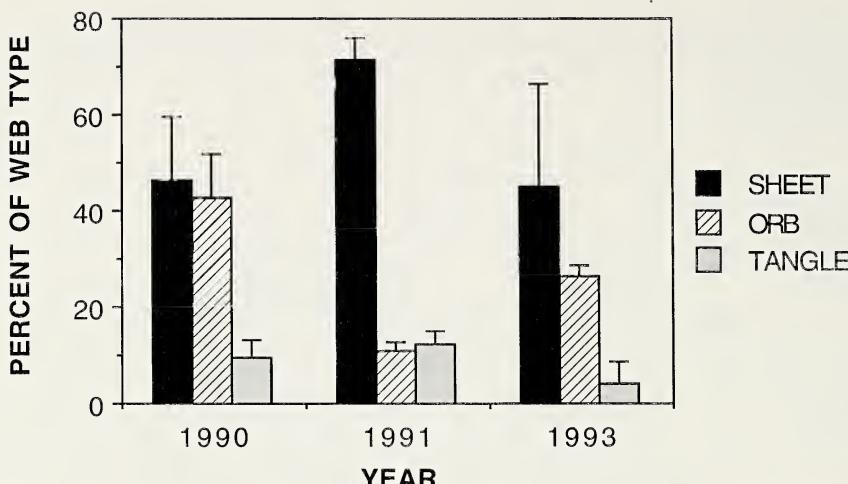
Figure 2.—The relative abundance (percent of all web-spiders found) of sheet, orb, and tangle webs that comprised the web-spider community in soybeans during the late season of three years.

The relative amount of weedy vegetation, leaf damage (which is a measure of the activity of herbivores) and web spiders in the late season across the three years of this study appear to be related. Weed abundance was a vegetation parameter that was different in all three years, and it had a strong positive correlation with spider abundance across years (Fig. 3) ($R^2 = 95.5$, $P < 0.05$). Leaf damage also differed among all years and it was negatively correlated with spider abundance (Fig. 4) ($R^2 = 79.5$, $P < 0.05$). Because of the strong correlation between weeds and spiders and between spiders and leaf damage, leaf damage was also negatively correlated with weed abundance in this data set ($R^2 = 74.0$, $P < 0.05$).

DISCUSSION

The phenology of web-spiders in these Ohio soybean fields was similar in many respects to that observed in other north temperate studies (LeSar & Unzicker 1978; Culin & Rust 1980; Culin & Yeargan 1983; Ferguson et al. 1984). The variation among years is interesting in that the overall abundance was different in each of the three years and that difference is not reflected
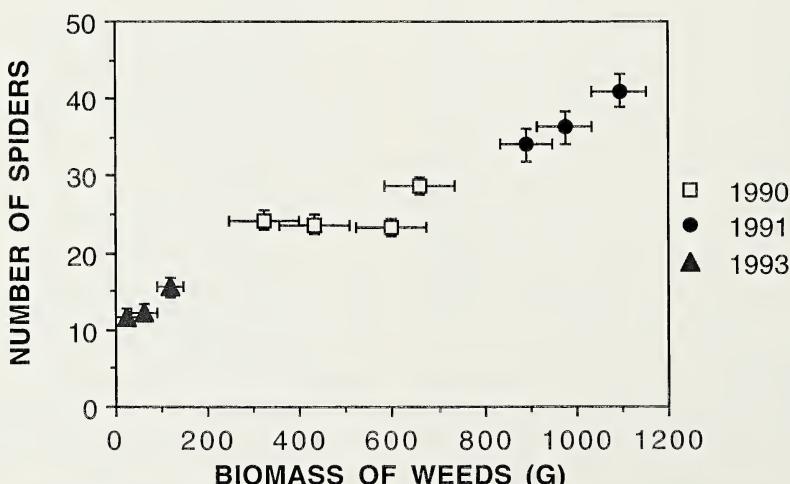
Figure 3.—The mean number of web spiders (per four one-meter row sections) found in the soybean fields late in the season as a function of the biomass of weeds surrounding one row meter.
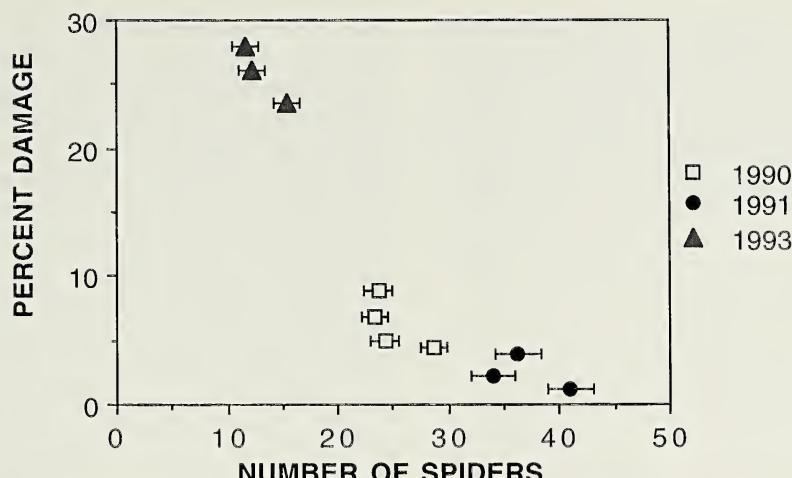
Figure 4.—Leaf damage (% removed by pest insects) experienced by soybean leaves as a function of the number of web-spiders (per four one-meter row sections) found in each field over three years.

by parallel differences in the web types we observed. For example, the highest overall spider abundance was in 1991 when sheet webs dominated the community but orb webs were much more abundant in 1990 (Fig. 2). LeSar & Unzicker (1978) observed that both *Tetragnatha laboriosa*, an orb weaver, and *Microlinyphia pusilla*, a sheet-web weaver, were more abundant in a dry year than they were in a second wetter year and they attributed this differences to a negative effect of rainfall on web spinners. The sheet-web weavers at our site appeared to follow that pattern in that they were much more abundant in 1991, the driest of the three years studied (J. Klink pers. comm.). However, orb weavers, including *T. laboriosa*, were most abundant in 1990 (Fig. 2) which was the wettest of the three years under study (J. Klink pers. comm.). In 1991,

sheet-web weavers were very abundant early in the season in relation to any other web type in any year (Table 3). It must be that, for some reason, they were able to disperse in precisely when microhabitat conditions were suitable and establish themselves in the fields early in that year. Since their webs are frequently three-dimensional and require multiple attachment sites, high sheet web densities could have inhibited the colonization of orb-weavers.

The lower numbers of spiders and differences in spider types present in the fields in 1990 than compared to 1991 may, in part, be due to the time of planting. The soybean season was about two weeks later in 1990 that in the other years (Table 1). Since colonization occurs largely by ballooning and the greatest peak of ballooning is observed early in the summer (Bishop & Riech-

Table 5.—Correlations between plant characteristics and web-spider abundance in soybean agroecosystems in 1990 and 1991.

Variable	Sign	R	df	P
1990				
Height	+	0.234	43	>0.1
Width	+	0.077	43	>0.1
Foliage height diversity	+	0.234	43	>0.1
1991				
Height	+	0.491	47	<0.01
Width	+	0.650	47	<0.01
Foliage height diversity	+	0.565	47	<0.01

ert 1990), more potential colonizers would have found suitable habitat in 1991 than in 1990. Likewise, the timing of planting may have coincided with the ballooning of sheet-web weavers to lead to a greater establishment of those spiders in that year. The season in 1993 was even earlier (Table 1) and the plants developed normally (Table 2), so this explanation for annual differences does not explain the overall low spider abundance observed in that year.

The specific development of the web-spider community was more closely aligned with various vegetational measurements in 1991 than in 1990 (Table 5). In many cases, the complexity of the habitat has been related to spider abundance (Greenstone 1984; Rypstra 1983, 1986; Döbel et al. 1990; Gunnarsson 1990; Uetz 1991). Yet in 1990 when overall spider abundance was lower, there were no significant correlations between spider abundance and plant structure (Table 5). The lack of any such correlations, might suggest that the habitat was not saturated, i. e., that there were suitable unused web sites. Alternatively, since sheet webs comprised such a large proportion of the web-spider community in 1991, it may be that our measures of vegetational complexity were better measures of habitat suitability for sheet-web weavers than for all web spiders (Fig. 2). One complication is that the overall spider community appeared to respond quite strongly across years to weed abundance which was also highest in 1991 (Fig. 3), yet our measures of vegetational heterogeneity focused specifically on the soybean plants and did not reflect changes in the developing weed community. The tighter correlations we observed in 1991 in comparison to 1990, may mean that sheet-web weavers were more dependent on the soybean plants themselves for web sites than the other spiders we observed.

Previous studies have demonstrated that spider numbers can be manipulated by altering the habitat structure available to them (Robinson 1981; Rypstra 1983; Carter & Rypstra 1995). Likewise, in no-till soybean systems, which tend to be more weedy than conventionally tilled fields, the greater diversity and abundance of beneficial arthropods, including spiders, have been attributed to the greater structural diversity of the plant community (House & Stinner 1983). Ferguson et al. (1984) found greater spider numbers and diversity in soybean fields that were planted closer together and disturbed less. Our data support those studies and suggest that high weed abundance is the basis for a more dense community of web spiders (Fig. 3).

It has been demonstrated that spiders can reduce the herbivory experienced by plants (Riechert & Bishop 1990; Carter & Rypstra 1995). The strong negative correlation between spider abundance and leaf damage we observed suggests that the spiders were having an impact on the action of herbivores in these fields as well (Fig. 4). We believe that weed abundance allowed a more dense community of spiders (Fig. 3) and that the reduction in leaf damage is due to the direct and indirect effects of the spiders on the herbivores. In experiments with introduced web-spiders in these same soybean fields, we observed a negative correlation between the biomass of prey killed by spiders and leaf damage experienced by plants in localized areas (Carter & Rypstra 1995). Therefore we think that it is likely that the differences in damage we observed across years in this study are due to differences in the spider community. However, one cannot ignore the correlation between weed biomass and leaf damage. Weeds may offer polyphagous pests an alternative food source and, in that way, reduce their dependence on the crop plants.

The results of studies on the interaction of weeds, foliage pest species, and crop plants are mixed, with some pest species inflicting more damage to the crop plants when weeds are abundant and some pest species inflicting less (Hammond et al. 1987; Stinner & House 1990). However, more frequently it has been suggested that the reduction in pest damage in no-till, and therefore weedy, agroecosystems is due to increased predation on or parasitism of herbivorous insects (Speight & Lawton 1976; House & Stinner 1983; Pavuk & Stinner 1992). Clearly more work is critically needed to uncouple these effects in order to understand the relationship between spiders, their prey and the plants in agroecosystems.

In summary these data suggest that agricultural systems contain highly variable dynamic web spider communities in which the composition parameters are related to vegetation development in some years. More information on the specifics of colonization and establishment of different spiders and their preferred plant associations are critical to understanding this system. These data underscore the importance of understanding such interactions since it is becoming increasingly clear that spiders are important predators that can influence the action of pest insects in agroecosystems.

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MECHANISMS OF THE FORMATION OF TERRITORIAL AGGREGATIONS OF THE BURROWING WOLF SPIDER *GEOLYCOSA XERA ARCHBOLDI* MCCRONE (ARANEAE, LYCOSIDAE)

Samuel D. Marshall[1]:   Department of Zoology & Graduate Program in Ethology, University of Tennessee, Knoxville, Tennessee 37996 USA

ABSTRACT.   It has long been proposed that aggregations of *Geolycosa* wolf spiders form by limited dispersal from the maternal burrow. In this study I test for conspecific attraction and limited dispersal to account for the formation and maintenance of aggregations of *Geolycosa xera archboldi* McCrone, endemic to the scrub habitats of Highlands County in central Florida, USA. I found no evidence for conspecific attraction in either field tests or observations of natural relocation. I did confirm that hatchlings disperse a short distance from the maternal burrow. The distance hatchlings disperse is influenced by territorial interactions with siblings. Older spiders which were experimentally released also exhibited limited dispersal.

Aggregation by territorial species presents a theoretical problem in that territoriality is by definition partitioning of space away from conspecifics. The hypothesized functions of territorial aggregation fall into two general categories: 1) 'dear enemies', where neighbors are beneficial and; 2) 'conspecifics-as-cues', where dispersing individuals use established conspecifics as cues to habitat quality.

Getty's (1981) competitive collusion model proposed that neighbors might ultimately serve to maximize territory size. This 'dear enemies' model suggests that individuals which settle next to neighbors will be less likely to lose territorial space to later immigrants to the patch. These later immigrants might insert their territories into the unclaimed space between randomly spaced territories and usurp peripheral space from these surrounding territories.

Conspecific attraction occurs when dispersing or relocating individuals use the presence of established conspecifics as site-selection criteria when they choose a site to establish a territory. The use of conspecifics as evidence of habitat quality was proposed as early as 1961 by Orians to explain the phenomenon of territorial aggregation by nesting red-winged blackbirds (*Agelaius phoeniceus*). Stamps (1987, 1988, 1991) has proposed this as the function of conspecific at-

traction by anole lizards (*Anolis aeneus*) on the Caribbean island of Grenada.

I have documented both territoriality and aggregation in *Geolycosa xera archboldi* McCrone, a burrowing wolf spider (Marshall 1994). Clumped dispersion of *Geolycosa* burrows has been noted previously (*G. rafaelana*, Conley 1984; *G. turricola*, Miller 1989; *G. missouriensis*, Richardson 1990). It has been proposed that aggregations of *Geolycosa* wolf spiders form by the settlement of juveniles near the maternal burrow (Miller 1989). However, this has never been quantified nor have alternative hypotheses been tested.

In this study I examine the mechanisms of aggregation formation in *Geolycosa xera*. *Geolycosa xera* is restricted to the scrub habitats of central Florida where it builds burrows in areas of exposed sand (Marshall 1994). These spiders are entirely dependant on their burrows for protection from predators and climatic extremes. All foraging activity is centered on the burrow mouth and *G. xera* does not leave the immediate vicinity of its burrow unless dispersing.

METHODS

The present study was conducted at Archbold Biological Station in Highlands County, Florida. Archbold is a private research facility approximately 10 km S of Lake Placid.

Experimental tests for conspecific attraction.—I tested for conspecific attraction in the summers of 1990 and 1991. I have previously

[1] Present address: Department of Zoology, Miami University, Oxford, Ohio 45056.

observed and quantified dispersal by these spiders in summer (Marshall in press). I used two approaches in my test for conspecific attraction: enclosure tests and field trials. In both these tests I examined the influence of established territory holders on burrow sites chosen by experimentally released individuals I will call 'settlers'. For the enclosure tests I built five 1.0 × 2.0 m aluminum flashing enclosures in an area of suitable microhabitat. The founding population was induced to dig burrows into the end of each enclosure I selected by covering the sand in the other end with leaf litter. I then removed the leaf litter and released one marked settler into each enclosure each night for a week at randomly selected points (using an X, Y coordinate system and a random number table). The morning after release I noted where the settlers had dug their burrows. Settlers which dug burrows in the half of the enclosure with the founders were scored as having exhibited conspecific attraction, and those settlers which had dug burrows in the other end as not exhibiting conspecific attraction.

For the field trials I created four rectangular, open sand patches 1.5 × 3.0 m in oak scrub by raking leaf litter and cutting vegetation to the ground surface, exposing the sand. Studies I have conducted on the ecology of *G. xera* indicate that barren sand is the sole requirement for burrow placement. Two of these were to be test patches with founders, and two were to be control patches without any founding population. Ten founders were established in one end of the founder patches in a two by five array. This founding group was established by setting out 5 cm diameter approximately 20 cm tall clear acetate cylinders spaced 30 cm apart and placing a spider into each cylinder at dusk. It was hoped at this time that they would dig a burrow. Individuals which did not dig a burrow by morning were removed and replaced with another spider the following evening. These cylinders were removed after the spiders built burrows. I used older spiders (burrow diameter > 5.0 mm) as founders, and younger spiders (burrow diameter < 3.0 mm) as settlers (this followed the finding that younger individuals relocate more often; Marshall in press). The distinct size difference between founders and immigrants made it unnecessary to mark the spiders. Over six successive evenings I introduced two settlers 1.0 m apart in the center of each sand patch (for a total of 12 per patch). The next morning I recorded the burrow sites (i. e., which end) they chose and

removed them. To test for non-random dispersal I scored site choice by which half of the patch the settlers dug burrows in. If the settlers were exhibiting conspecific attraction they should preferentially choose the ends of the patches with founders. In the patches with no founding population settlement should be random. To test for non-random settlement I used a Fisher's exact test on frequency of burrow site choice scored by which end of the patch immigrants selected for each pair of patches for each treatment. In the founder patches this was either the half with founders or the half without founders. In the control patches this was either the eastern end or the western end.

Census studies of immigration and recruitment. — In order to test for the influence of local population density on rates of immigration (spiders moving into the area) and recruitment (spiders hatching within the area), I collected census data on naturally-occurring local populations of *G. xera*. I set up 10 pairs of 1.0 m² quadrats in 10 independent patches of sand in the scrub. A patch was considered independent if it had a well-defined leaf litter edge. I selected each census quadrat pair to represent the highest and the lowest spider densities found within each patch. I censused these patches on a weekly basis from 2 April–10 July 1993. At each census new burrows were flagged and measured. Based on observations of natal dispersal, I knew that all spiders with a burrow diameter of 2.0 mm or less were spiderlings and assigned them to the 'recruit' category (in the sense of recruitment into the population by birth). All new spiders with larger burrows were considered to be settlers. Also, previous research (Marshall in press) has shown that these spiders will periodically close their burrows and that 90% of these closure periods will last 14 days or less. For this reason I will consider only the census data from 16 April–10 July in my analysis in order to minimize the counting of residents as settlers when they reopen their burrows during the early part of the census period. At each census any previously flagged burrows were checked, and it was noted whether they were open or closed. These data allow for an estimation of rates of immigration versus recruitment.

Dispersal strategies. — Aggregations of *Geolycosa* wolf spiders have been proposed to form by the settlement of hatchlings in the vicinity of the maternal burrow (Conley 1984; Miller 1989). I tested this by recording the dispersal distances

of hatchlings from five separate sibling groups. I began by observing the burrows of females I knew to be incubating eggs in late June 1991. When I first observed spiderlings in the maternal burrow, I began to check the vicinity of the maternal burrow daily for the appearance of spiderling burrows. I measured the distances of each spiderling burrow from the maternal burrow, its nearest-neighbor distance and its nearest-neighbor's burrow mouth diameter (burrow mouth diameter is closely correlated with body size in *Geolycosa*; McQueen 1983; Miller & Miller 1984; Marshall in press). As the maternal burrows were spaced widely apart, I feel confidant that all observed spiderlings were attributed to the appropriate maternal burrow. In order to look for pattern in the data, I used regression analysis of the distance dispersed as a function of days since the onset of dispersal. I predicted that a significant, positive relationship between day and distance dispersed would be evidence of territorial aggregation by the spiderlings. Individuals which dispersed first would establish territories close to the maternal burrow. Siblings that dispersed later would be forced to walk further before digging a burrow by competition for space with previously settled siblings. Only the data from the first 10 days were used in order to limit the recounting of relocating spiderlings. Counting spiderlings twice would violate the assumption of independence of the regression model.

The high rate of relocation found in the 1991 summer field season (up to 3.2% of the population relocates per day; Marshall in press) coupled with the persistence of aggregations raised the question of how individual dispersal strategies might influence patterns of dispersion. In June of 1994 I marked and released 80 individuals in order to quantify individual dispersal distance. The test subjects were juveniles arbitrarily collected from outside the study population. I marked the spiders with a fluorescent powder (Radiant Color, Magruder Color Co., Elizabeth, New Jersey) of a type which has been widely used for both invertebrates and vertebrates (Lemen & Freeman 1985; Fellers & Drost 1989; Morse 1993). I marked the spiders by placing them in a vial containing a small amount of the powder and gently shaking them so as to completely coat the spider. Spiders were held until release in a clean vial. One advantage the use of this powder has over paint marking is that the spiders incorporate the powder coating their bodies into their new burrows. These colored burrow mouths

are very conspicuous in the white sand of the scrub. The spiders were released at sites in suitable habitat at least 30 cm from larger conspecifics. I did this to reduce the chance of cannibalism due to my choice of release site. I released the spiders in early evening (approximately 1800 h) which is the time of day I had most commonly observed relocating individuals. Spiders were released by placing the vial containing the spider open on its side in the sand and then leaving the area. I found burrow sites the next morning by searching the entire sand patch.

I also marked, released, and watched 14 additional individuals until they dug burrows. These individuals were marked with enamel paint on the carapace and released as detailed above. Instead of leaving the area I stepped back to observe from at least 4 m away.

RESULTS

Experimental tests for conspecific attraction.—In the enclosure test there was no evidence for conspecific attraction. The mean proportion of settlers in the five enclosures choosing the end of the enclosures with founders was close to one-half (0.44).

There was no evidence for conspecific attraction in the field trials either. In both the patches with founders and without, settlers settled randomly (Fisher's exact test: patches without founders, $P = 0.54$; patches with founders, $P = 0.19$).

Census studies of immigration and recruitment.—The mean densities for the weekly censuses of the paired plots were significantly different for high versus low density local populations (paired $t = 5.84$, $df = 9$, $P < 0.001$). However, there was no significant difference for immigration rate (paired $t = 1.08$, $df = 9$, $P >$

Table 1.—Summary of regression analyses of natal dispersal of 5 groups of *Geolycosa xera archboldi* at Archbold Biological Station. For the analyses the distance from the maternal burrow that spiderlings built burrows was regressed on the number of days since the initiation of dispersal by the brood that the spiderling burrow appeared.

	N	Sig.	r^2
First group	24	$P = 0.01$	0.26
Second group	19	$P = 0.001$	0.63
Third group	51	$P = 0.006$	0.14
Fourth group	20	$P = 0.0043$	0.37
Fifth group	22	$P = 0.0006$	0.45
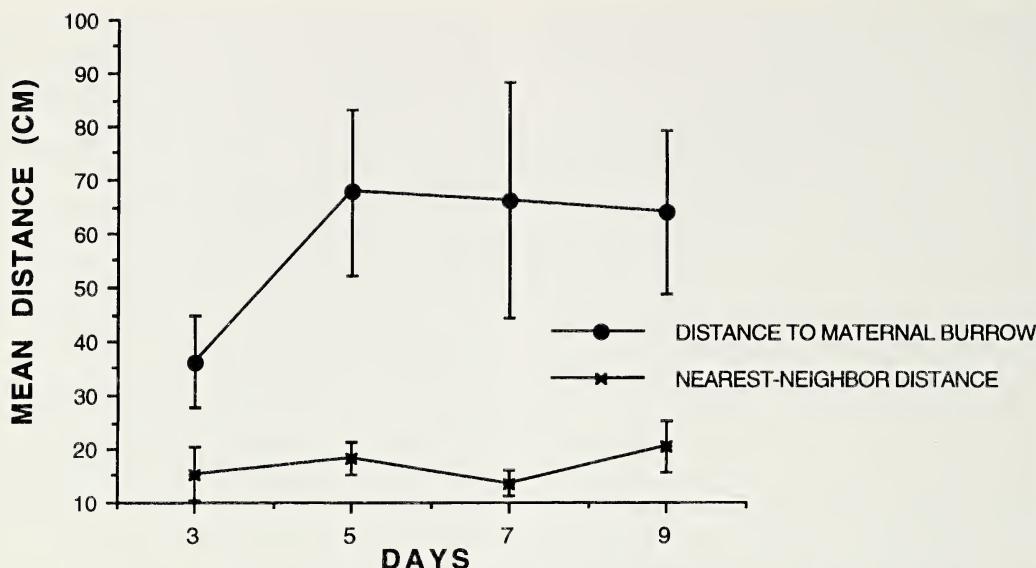
Figure 1.—Cumulative mean dispersal distances (± SE) for five cohorts of hatchling *Geolycosa xera archboldi* at Archbold Biological Station, June-July 1991. The two lines represent the mean of values recorded for each spiderling burrow, the standard errors are for an *n* = 5 (for the five cohorts).

0.2) or recruitment rate (paired *t* = 0.04, *df* = 9, *P* > 0.5).

Dispersal strategies.—In all five groups of hatchlings, there was a significant positive correlation between the days since the initiation of dispersal and the distance dispersed (Table 1). The low R^2 values may be attributed to the spread of distances dispersed on the later dates. While the nearest-neighbor distance remained relatively constant, the distance from the maternal bur-
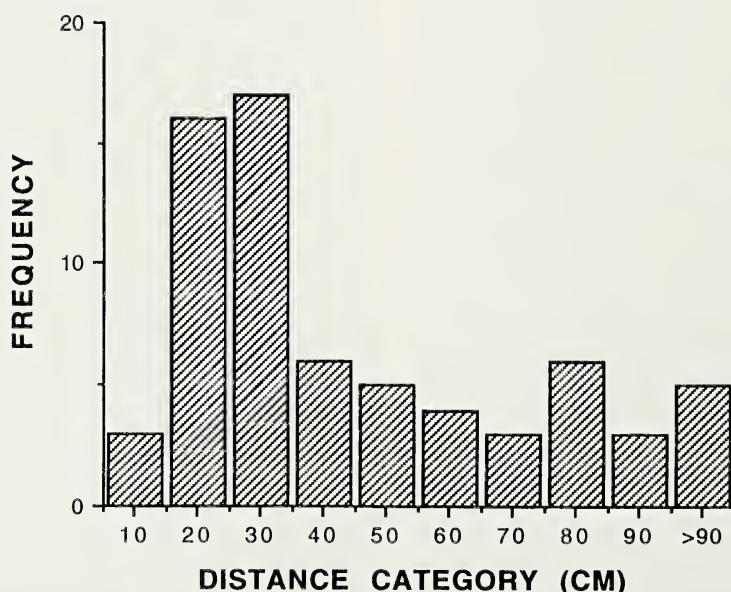
Figure 2.—Frequency distribution of dispersal distances for 68 marked juvenile *Geolycosa xera archboldi* at Archbold Biological Station, June 1994. Distances are from release site to new burrow site.

row increased sharply between days 3 and 6 (Fig. 1). Almost all of these nearest-neighbors were siblings.

I found 68 of the 80 spiders I released. The marked spiders dispersed an average of 43.9 cm before building a burrow (Fig. 2, 43.9 ± 38.4 cm, $n = 68$, range 7–240 cm). My failure to find 12 of the released animals will bias my results to the shorter distance categories as these individuals are likely to have dispersed further than most (an artifact of my own searching behavior).

Out of the 14 experimentally released spiders, 10 settled while under observation. The time to initiate burrow construction was 48:32 ± 15:23 min:sec (mean ± 1 SD). The remaining four took longer than 90 min, and I found them in new burrows the next morning.

DISCUSSION

Territorial aggregations of *G. xera* initially form and are maintained by limited dispersal. Spiderlings leaving the maternal burrow apparently disperse only as far as they have to avoid their territorial siblings. I found no evidence for conspecific attraction in this spider. However, aggregations persist in spite of relocation rates as high as 3.2% a day (Marshall in press). The reason for this seems to be the limited dispersal that these spiders exhibit even when relocating. *Geolycosa xera* is highly mobile on the sand (being an ambush predator), yet over half these spiders settled within 30 cm of the release site. I believe that this limited dispersal is an evolved strategy rather than a maladaptive lack of vagility. Dispersal is assumed to be riskier than non-dispersal (Southwood 1962; Gaines & McClenaghan 1980; Johnson & Gaines 1990). In the case of *G. xera*, an important potential cost of dispersal is the risk of mortality due to cannibalism. *Geolycosa xera* periodically close their burrows (e. g., when molting or after catching a large prey item). These periods of burrow closure last up to two weeks or longer (Marshall in press). Apparently dispersing individuals are unable to assess the location of the closed burrow of a larger conspecific, and I have seen smaller spiders settling within the territory of larger individuals with closed burrows. The correlation of the abandonment of the burrow of the luckless settler with the re-opening of the larger resident's burrow is suggestive. This uncertainty associated with site choice underlies the risk of relocation, making it analogous to dispersing in a mine field. I found no evidence for any ecological predictors of burrow site location within the microhabitat (Marshall 1994). Thus, given open sand, I hypothesize that burrow sites are chosen only to avoid active larger conspecifics. There is no advantage to long-distance dispersal, given the uncertainty of the location of closed burrows and the risk implicit in crossing space defended by potentially cannibalistic territory holders.

While inbreeding has been hypothesized as a cost of limited dispersal (Johnson & Gaines 1990), it is not likely an issue for *G. xera*. When male *G. xera* mature, they abandon their burrow and wander in search of mating opportunities. I have observed wandering adult male *G. xera* to move between patches, which I have not observed natal dispersers to do. Presumably, the greater distances travelled by the males in search of matings reduce the probability of inbreeding within these patches of microhabitat.

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A COMPARISON OF POPULATIONS OF WOLF SPIDERS (ARANEAE, LYCOSIDAE) ON TWO DIFFERENT SUBSTRATES IN SOUTHERN FLORIDA

David B. Richman: Dept. of Entomology, Plant Pathology and Weed Science, New Mexico State University, Las Cruces, New Mexico 88003 USA; **Jan S. Meister**[1]: Dept. of Entomology and Nematology, University of Florida, Gainesville, FL 326112; **Willard H. Whitcomb**[2]: Dept. of Entomology and Nematology, University of Florida, Gainesville, Florida 32611, and **Leigh Murray**: Dept. of Experimental Statistics, New Mexico State University, Las Cruces, New Mexico 88003 USA

ABSTRACT. Wolf spiders were sampled from sandy and grassy substrates every month for one year at Archbold Biological Station, Lake Placid, Florida, from December 1981 through November 1982. It was found that the faunas were different in species composition, even though they were within a few meters of one another. Light-colored species, such as *Lycosa ceratiola* and *Lycosa osceola*, were more abundant on or restricted to the sandy surface, while darker colored species, such as *Lycosa miami, Lycosa annexa, Lycosa abdita* and *Schizocosa crassipes* were more abundant on or restricted to, the grassy substrate. A total of twelve species of lycosids were collected.

Archbold Biological Station currently contains 2023.5 hectares of Lake Wales Ridge scrub, dominated by slash pine, *Pinus elliotti* Engleman, sand pine, *Pinus clausa* (Engleman) Sargent, several species of scrub oaks, *Quercus* spp., saw palmetto, *Serenoa repens* (Bartr.) Small and *Sabal etonia* Swingler ex. Nash, among others (Vander Kloet 1979). The scrub region of south Florida is unique and the largest part of the remaining scrub on the Lake Wales Ridge occurs on the station. The wolf spider fauna is highly varied and contains some unique or nearly unique elements, such as *Sosippus placidus* Brady and *Geolycosa xera* McCrone (Franz 1982). Richman (1984) listed 15 known species for Highlands County. Most of the species involved are little known, other than their original descriptions. Two of the species which were recorded in the list are very abundant at the station. These are *Lycosa ceratiola* Gertsch & Wallace and *Lycosa miami* Wallace. Wallace (1942) included *L. miami*, but not *L. ceratiola*, in the *lenta* group; but both appear to be related, based on their morphology. An observation was made in 1981 by Richman and Whitcomb that there seemed to be a differ-

ence in the lycosid fauna on sand compared with the fauna on grass. To document this difference we decided to sample wolf spider populations on both substrates monthly for a year and then compare the results to test the hypothesis that there was a distinct difference between the faunas and that it persisted throughout the annual cycle.

METHODS

An area immediately adjacent to and south of the main building at Archbold Biological Station (27°20′N, 81°20′W) was selected for accessibility and for the presence of both grassy areas and sandy areas. The areas were approximately 10 × 100 m (1000 sq. m) and were perpendicular to each other. The grassy area was just south of the main building and was oriented along a north-south line, whereas the sandy area edge was just south of the south edge of the grassy area and was oriented along a east-west line (Fig. 1). Both substrates were sampled monthly at night from December 1981 through November 1982 (Table 1), using headlighting techniques (Wallace 1937). A minimum of 50 spiders was collected on each substrate during each sampling period (total minimum of 100 spiders/month), except for the first sample (December 1981) when a minimum of 24 was collected on each substrate and for grass in September 1982 when 29 were collected. Depending on the number of people searching

[1] Current address: 11004 SW 67th St., Gainesville, Florida 32608.
[2] Current address: 4013 NW 39th Way, Gainesville, Florida 32606.

and the time of year, the samples were collected in anywhere from 10 minutes to two hours, but usually took 20–30 minutes. We used a relatively standard number of spiders because it was felt that this would give us a relative proportion of adults and immatures. At no time did we attempt to obtain absolute densities. Because the eye shine was used to collect all samples in both cases, rather than just searching for spiders, we feel that the proportions reasonably reflected the populations present on the substrates. While the sand had little vegetation on it, the grass was short on the grassy area and presented no problems in seeing the eye shine. The spiders were preserved in alcohol and later identified and each carapace width measured (including immature specimens). Identifications were made by Allen Brady, Hope College, Holland, Michigan; G. B. Edwards, Florida State Collection of Arthropods, Gainesville, Florida; and the senior author. Once adults were identified, it became possible to at least tentatively identify the majority of the immature specimens. Most of the immature specimens were identified by the senior author. Weather data were provided by Archbold Biological Station. Samples of specimens collected are deposited at the Archbold Biological Station (complete synoptic collection), the Arthropod Museum of New Mexico State University (partial synoptic collection), and the Florida State Collection of Arthropods (partial synoptic collection and most extra and immature specimens).

Statistical analyses included preliminary frequencies and time plots for counts of each species
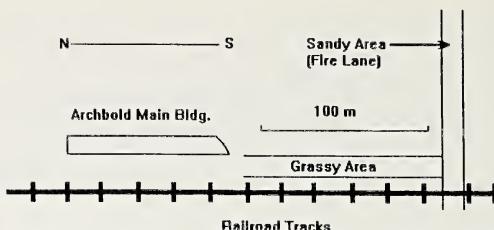
Figure 1.—Map of Archbold Biological Station main building area, showing the two study sites. Scale is approximate. Map modified from Abrahmson et al. 1984.

and substrate combination. Also chi-square tests of homogeneity were conducted to compare occurrence of different species. These chi-square tests included: substrate by month comparisons for each species; substrate species comparisons for each month; and month by sex comparisons for each substrate and species combinations. Problems were experienced with sparseness in chi-square tables due to low counts for all but two species and all sexes. Finally, an analysis of variance was performed for each substrate and species combination to compare average size over months. All analyses were performed using SAS© (SAS Institute 1989, 1990).

RESULTS

A total of five species of *Lycosa*, three species of *Rabidosa*, one species of *Gladicosa*, one species of *Pardosa*, one species of *Sosippus*, and one species of *Schizocosa* was collected at the study site over the year (Table 2). Of these, eight species

Table 1.—Collecting dates for *Lycosa* spp. at Archbold Biological Station, Highlands County, Florida (1981–1982). * Two teams used.

| Date | Time of collection | |
	Grass substrate	Sand substrate
17 December 1981	Approximately hour after sundown	
21 January 1982	7:00–7:20 P.M. EST*	7:20–7:36 P.M. EST
22 February 1982	7:30–8:00 P.M. EST	8:00–8:30 P.M. EST
22 March 1982	7:45–8:05 P.M. EST	8:05–8:30 P.M. EST
20 April 1982	7:50–8:20 P.M. EST	8:25–8:55 P.M. EST
19 May 1982	9:05–9:15 P.M. EDT	9:15–9:30 P.M. EDT
21 June 1982	9:00–9:30 P.M. EDT	9:30–10:00 P.M. EDT
22 July 1982	9:00 PM EDT*	9:00 P.M. EDT*
18 August 1982	9:20–1:15 P.M. EDT	8:35–9:20 P.M. EDT
20 September 1982	8:30–9:30 P.M. EDT*	8:30–9:30 P.M. EDT*
26 October 1982	Approximately hour after sundown	
22 November 1982	Approximately hour after sundown	
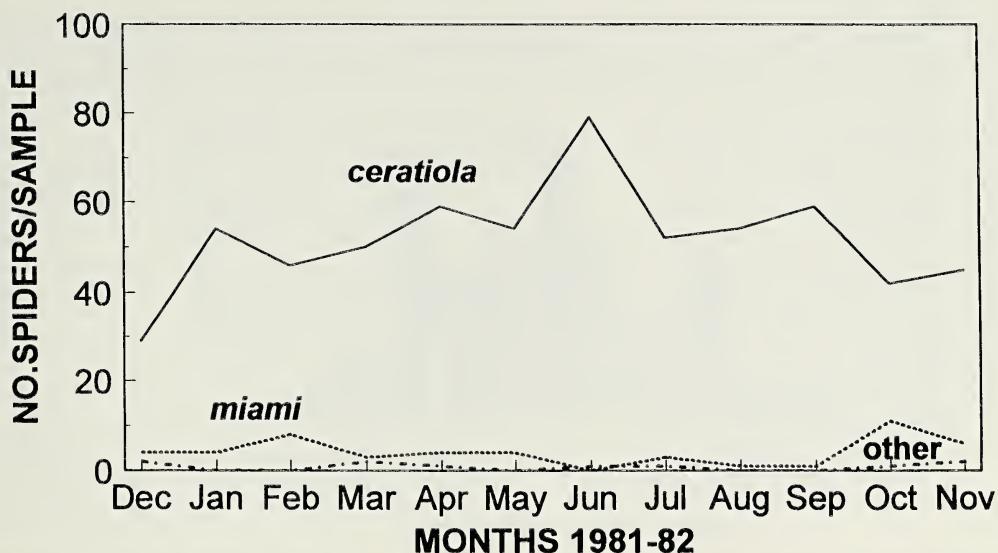
Figure 2.—Numbers of *Lycosa ceratiola*, *Lycosa miami* and other lycosids on sand at Archbold Biological Station, Highlands County, Florida, December 1981 to November 1982.

were not listed by Richman (1984). Only two of the species collected in this study, *L. ceratiola* and *L. osceola*, were in the Archbold Biological Station Collection at the time of the study. In addition to the wolf spiders, at least one immature specimen of the giant crab spider, *Heteropoda venatoria* (Linnaeus), and one of an unidentified gnaphosid were collected on the grassy surface over the year.

The chi-square test of homogeneity of occurrence of species on the two substrates indicated that there was indeed a significant difference ($P < 0.005$ for all months) between the frequency of *Lycosa ceratiola* and *Lycosa miami* on the two substrates. Only the samples from August were questionable because 25% of the cells had expected counts of less than five. This sparseness was a common problem when more than these
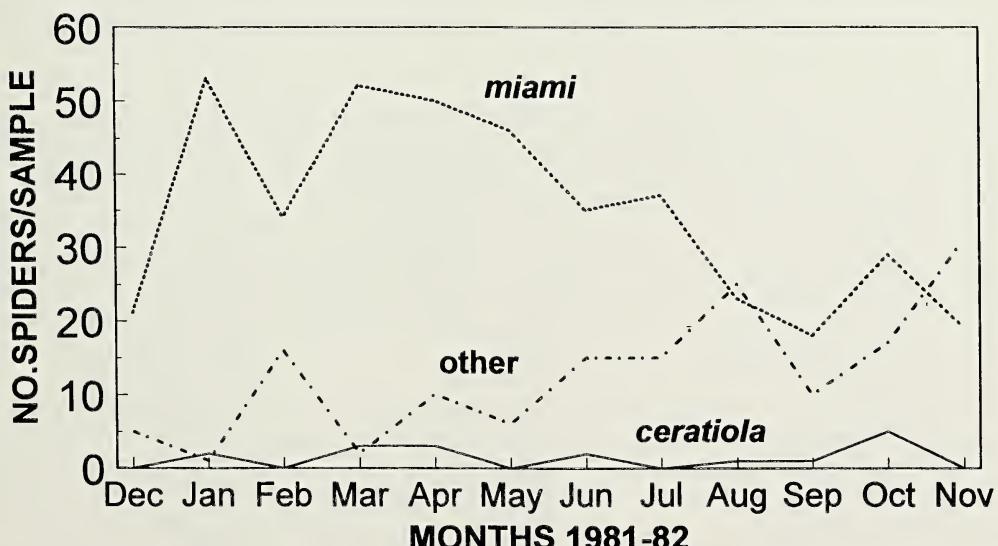
Figure 3.—Numbers of *Lycosa ceratiola*, *Lycosa miami* and other lycosids on grass at Archbold Biological Station, Highlands County, Florida, December 1981 to November 1982.
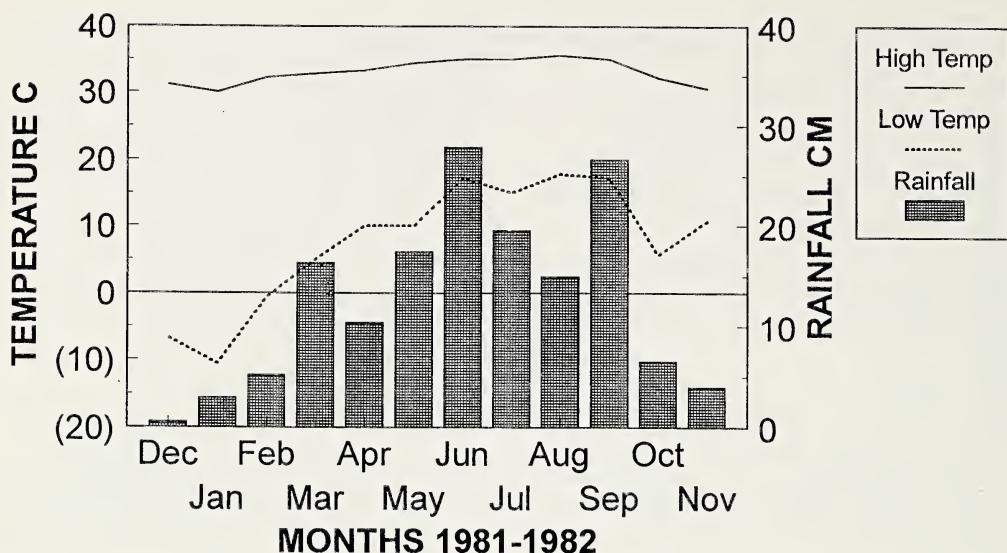
Figure 4.—Weather data for Archbold Biological Station, Highlands County, Florida, December 1981 to November 1982. Temperatures are averages for each month in °c. Rainfall is total for month in cm.

two species were included in the analysis, even though it is evident that there is a real difference between the species recovered on sand and those recovered on grass. Thus, no statistically valid conclusions can be made about the other species.

Monthly counts (Figs. 2, 3) for the two species demonstrate this distinct difference very well. It is quite obvious that the sandy colored *L. ceratiola* preferred sandy substrates, while the darker *L. miami* preferred the grassy substrate.

Size analysis was only meaningful for *L. ceratiola* on sand and *L. miami* on grass. These were

present throughout the 12 months of the sampling period. The average carapace width for these two species each month is shown in Table 3. It is curious that while immatures were present at all times of the year, adult males of *L. miami* were found in only four scattered months (December, March and July–August). Adult females of *L. miami* were collected in December and March–August, whereas males of *L. ceratiola* were collected from March–July and females in January and March–November (Table 3).

Some prey records were obtained, especially

Table 2.—Species of *Lycosa* and other Lycosidae collected at Archbold Biological Station, Highlands County, Florida, 1981–1982. Specimens of *Lycosa ceratiola* and *Lycosa miami* include those collected on both sand and grass and so do not match totals in Table 3. Identifications were by Allen Brady, G. B. Edwards and D. B. Richman. Species with "*" were not listed by Richman (1984).

Species	Substrate	n and sexes
Gladicosa pulchra (Keyserling)*	Grass	1♂
Lycosa abdita Gertsch*	Grass, sand	2♂, 10♀, 3 imm.
Lycosa annexa Chamberlin & Ivie*	Grass	23♂, 13♀, 41 imm.
Lycosa ceratiola Gertsch & Wallace	Sand, grass	23♂, 55♀, 561 imm.
Lycosa miami Wallace	Grass, sand	12♂, 22♀, 432 imm.
Lycosa osceola Gertsch & Wallace	Sand (1 on grass?)	3♀, 2 imm.?
Pardosa littoralis Banks*	Grass	1♂, 1♀, 5 imm.
Rabidosa hentzi (Banks)*	Grass (2 on sand)	1♂, 7 imm.
Rabidosa punctulata (Hentz)*	Grass	1♀, 3 imm.
Rabidosa rabida (Walckenaer)*	Grass	2 imm.
Schizocosa crassipes (Walckenaer)*	Grass (1 on sand)	3♂, 10♀, 12 imm.
Sosippus floridanus Simon	Grass	1 imm.

Table 3.—Mean carapace width (mm) for *Lycosa ceratiola* on sand and *Lycosa miami* on grass at Archbold Biological Station, December 1981 to November 1982. Adult males and females present in the sample are noted by the symbols ♂ or ♀.

Date	*Lycosa ceratiola* (*n*) (Range) (SD)	*Lycosa miami* (*n*) (Range) (SD)
December	3.10 (29) (1.17–5.67) (1.36)	3.80 (21) (1.67–8.17) (1.91) 1♂, 1♀
January	2.62 (54) (1.17–5.83) (1.21) 2♀	2.66 (53) (1.33–5.17) (0.83)
February	2.50 (46) (1.00–5.50) (1.05)	2.38 (34) (1.50–5.00) (0.77)
March	4.01 (50) (1.16–7.50) (1.62) 8♂, 4♀	3.59 (52) (1.83–7.83) (1.39) 1♂, 2♀
April	3.66 (59) (1.50–6.50) (1.47) 2♂, 4♀	4.06 (50) (1.83–8.83) (1.39) 4♀
May	3.68 (54) (1.67–6.67) (1.33) 1♂, 3♀	4.23 (46) (2.50–8.67) (1.30) 1♀
June	4.43 (79) (1.00–7.50) (1.82) 6♂, 16♀	4.04 (35) (1.33–7.33) (1.74) 2♀
July	3.36 (52) (1.33–7.00) (1.67) 4♂, 8♀	5.25 (37) (1.67–8.50) (1.91) 6♂, 7♀
August	2.74 (54) (1.67–7.33) (1.14) 4♀	4.48 (23) (1.50–7.83) (2.04) 4♂, 4♀
September	2.56 (59) (0.83–5.33) (1.33) 4♀	5.37 (18) (1.67–7.00) (1.12)
October	3.10 (42) (1.17–5.33) (1.15) 1♀	3.28 (29) (0.83–6.67) (1.44)
November	3.39 (45) (1.33–6.00) (1.35) 5♀	2.90 (19) (1.17–5.33) (1.17)

for *Lycosa ceratiola*. On 20 April 1982 at least 10 individuals of this species were collected with alates of the fire ant *Solenopsis* sp. (Formicidae). The same collection produced a click beetle (Elateridae), a scarab beetle *Ataenius platensis* (Blanchard) (Scarabaeidae) and a leafhopper, *Draeculacephala inscripta* Van Duzee. On 22 July 1982 individuals of *L. ceratiola* had caught a muscid fly, two scarabs and a mirid bug in the genus *Lygus*. On the 18 August 1982 a *L. ceratiola* was taken with a beetle fragment. On the same date a specimen of *L. miami* had captured a rove beetle (Staphylinidae). On 22 October 1982, a record for made of *L. miami* with a male gryllid cricket, and on 22 November, with one psychid larva and a myrmycine ant.

Weather data are summarized in Fig. 4. The lowest temperature was −11 °C in January 1982 and the highest was 35.6 °c in August. The highest rainfall was in June (27.85 cm) with the second highest in September (26.63 cm). December 1981 had the lowest rainfall (0.55 cm). With the exception of the cold periods in January and December (to −6.7 °c), the weather was very mild, even at night, and spiders were always found.

DISCUSSION

With these results we can make the following statements: 1), *Lycosa ceratiola* is most often found on the sandy substrate where it is most likely to be cryptic; 2), Conversely, *Lycosa miami* is most often found on the grassy substrate where it is most likely to be cryptic; 3), The grassy substrate has a higher species diversity (2:1) than the sandy substrate; 4), There were also more specimens of species that were found on both substrates (other than *L. ceratiola*) on grass than on sand; 5), The size analysis indicated that the various sizes were spread through the year, but that the smallest spiderlings were found in August for *Lycosa ceratiola* and in September for *Lycosa miami*. However, average carapace widths were the smallest for both species in February (Table 3). The low carapace widths in winter reflects the lower number of adults and the high numbers of (probably) third instar spiderlings. Thus most egg sacs were probably produced from the late summer and fall, although this may have been somewhat more spread out than for more northern species; finally, 6), prey, especially of *L. ceratiola*, appears to be quite varied and includes ants, beetles, crickets, true bugs, leafhoppers and caterpillars. Alate ants are readily attacked during mating flights.

The apparent crypsis of the two major species of *Lycosa* may be somewhat puzzling, as these are obviously nocturnal spiders. However, it might be noted that on moonlight nights the sandy color of *L. ceratiola* made it nearly invisible, whereas specimens of *L. miami* were visible as almost shadow-like bodies against the white sand. The reverse was true on the grassy areas. Thus the crypsis may serve to conceal the spiders from attack by vertebrate predators, especially night birds, such as screech owls, which are known predators of large lycosid spiders (Ross 1969).

The lack of female spiders carrying spiderlings or eggs is possibly a result of the larger, commoner (*lenta* group) species staying in their burrows during the egg laying and early spiderling

stages and, in the case of the smaller, rarer, species, may be a result of the low numbers taken. It is well established that members of the *lenta* species group are burrowers (Wallace 1942; Gertsch 1979). The less-collected species, some of which normally carry their eggs and first instar young with them, rarely came out on the grassy or sandy areas, but primarily stay on surfaces under the scrub canopy. The one specimen of *Sosippus* collected was obviously a stray, as these spiders build funnel webs in litter and shrubs (Brady 1962). Also, since only a few of the burrowing *Lycosa osceola* were collected, even on sandy surfaces, it is thought that they may have preferred sandy areas between plants in the nearby scrub. The scrub habitat was not sampled during the study, partly because of the difficulty of headlighting in that habitat. However, *L. osceola* was seen in the spaces between scrub plants on several occasions.

The fact that some large species of *Lycosa* differ in their substrate preference has been demonstrated in the past for two members of the *lenta* group, *L. lenta* Hentz and *L. ammophila* Wallace (Harper 1971). In these species *L. lenta* preferred leaf-litter and *L. ammophila* preferred sand. As noted earlier, Wallace (1942) placed *L. miami*, but not *L. ceratiola,* in the *lenta* group. It seems likely, from our observations and from the apparently similar morphology and appearance (especially the structure of the male palpi, female epigyna and general color pattern– *L. ceratiola* looks much like a very pale *L. miami*), that these two species, like *L. lenta* and *L. ammophila,* belong in the same species group. Where these "*Lycosa*" species will eventually be placed is unclear at the present time. However, it seems to be evident from both Harper (1971) and the current study that the various species of lycosids do partition their habitats in peninsular Florida.

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OBSERVATIONS ON THE NATURAL HISTORY
OF AN *UMMIDIA* TRAPDOOR SPIDER
FROM COSTA RICA (ARANEAE, CTENIZIDAE)

Jason E. Bond[1] and **Frederick A. Coyle**: Department of Biology, Western Carolina University, Cullowhee, North Carolina 28723 USA

ABSTRACT. An *Ummidia* trapdoor spider species near San Vito, Costa Rica, prefers steep slopes and open, sparsely wooded, early successional stage habitats. This habitat preference and the paucity of small juvenile burrows near adult burrows are consistent with spiderling dispersal by ballooning, known to occur in other *Ummidia* species. The entrance and burrow architecture and prey capture and defensive behavior of this species are similar to those of the few other observed *Ummidia* species. *Ummidia*'s door-holding defensive behavior is described in detail for the first time. Two enigmatic phenomena were observed: door hinges were often tilted well away from the horizontal plane, and one spider was found on two successive afternoons with the anterior half of its body fully exposed as it held onto the inner surface of its fully open trapdoor.

The trapdoor spider genus *Ummidia*, which is distributed widely across the southern United States and south through Mexico, the Caribbean, and Central America (Raven 1985), may contain as many as 100 species (N. Platnick pers. comm.). Scattered accounts of burrow structure and construction behavior (Moggridge 1873; Atkinson 1886a, b, c; Coyle 1981), ballooning (Baerg 1928; Coyle 1985; Coyle et al. 1985), prey capture (Coyle 1981), and other facets of *Ummidia* natural history (Gertsch 1979; Coyle 1981) have been published. We report here the first observations of the biology of a Central American species, probably *Ummidia rugosa* (Karsch 1880).

METHODS

Spiders were studied on the grounds of the Las Cruces Field Station of the Organization for Tropical Studies near San Vito, Puntarenas Province, in southwestern Costa Rica near the Panama border. The station is located at an elevation of 1095 m, receives an average of 3600 mm of rain per year, and includes a remnant (about 100 ha) of old-growth premontane rain forest, the once widespread climax ecosystem of the region. Our observations were made on 2–3 March 1992, 3–6 March 1993, and 5–7 March 1995 during the dry season, which lasts from January through March. Four burrow entrances

[1]Current address: Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0406 USA

were observed by Coyle in 1992, 16 by Bond in 1993, and 31 by Coyle in 1995. Most entrances studied in 1992 and 1993 were observed and measured again in the subsequent studies. One adult female burrow was excavated, measured, and photographed in each year. Drawings of the body and spermathecae of the adult female collected in 1993 (Figs. 1, 2) and the following description of this and a second (gravid) female collected in 1995 will help identify the species. Both specimens are deposited in the American Museum of Natural History. All measurements are given in millimeters. Values for the gravid female are in parentheses.

Body length (not including chelicerae) 20.7 (21.4). Carapace 10.02 (9.21) long, 8.52 (7.89) wide. Abdomen 11.52 (12.69) long, 8.02 (8.71) wide. Deep procurved thoracic groove, 1.84 (1.72) wide and 6.72 (5.98) from anterior margin of carapace. Carapace uniform chestnut brown, pars cephalica with median longitudinal row of strong setae flanked by two longitudinal clusters of setae. Eye diameters: AME 0.28 (0.20), ALE 0.62 (0.57), PME 0.26 (0.22), PLE 0.28 (0.22). Eye interdistances: ALE-ALE 0.90 (0.86), AME-AME 0.24 (0.17), AME-ALE 0.44 (0.31), AME-PME 0.20 (0.18), ALE-PLE 0.18 (0.20), PLE-PLE 1.34 (1.14), PME-PME 0.68 (0.60), PME-PLE 0.10 (0.08). Endites, labium, and sternum light brown. Sternum 5.56 (4.90) long, 5.23 (4.73) wide. With 5–8 slit sensilla scattered on each side of sternum. Legs dark brown, no distinct markings. Pro- and retromargins of chelicerae each with 8–10 teeth.

Leg formula IV-I-II-III, with leg II only slightly longer than leg III. Leg I article lengths: coxa 3.24 (2.68), trochanter 1.41 (1.04), femur 5.98 (5.40), patella 3.74 (3.20), tibia 3.98 (3.56), metatarsus 2.49 (2.02), tarsus 1.58 (1.30). Many trichobothria and 2–8 club-shaped bothria dorsally on tarsus of each leg. Three to five club-shaped bothria on dorsal surface of palpal tarsi.

MICROHABITAT, HABITAT, AND DEMOGRAPHY

Burrows were found only on steeply sloping (60–90°) earthen trail banks, not on gently sloping or level ground. No burrows were found during a careful 30 min search on hands and knees for entrances in the level lawn immediately above the bank where most burrows occurred. The apparent preference of these spiders for steep banks, a preference not exhibited by western North Carolina *Ummidia* (which are typically found on level and gently sloping ground), may be the result of the heavy rains experienced by the Costa Rica population selecting against any proclivity to construct burrows in flood-prone ground. All but five of the burrows were situated in stable soil partly covered with moss and sheltered from rain and runoff by overhanging roots or other materials. The entrances of burrows found in less sheltered microhabitats showed evidence of erosion damage; two of these projected nearly 20 mm above the surrounding soil.

Most burrows were located on the non-forested grounds of the Station along the end of the trail leading to the "Mirador." The rest were located in very young second growth forest within 20 m ("Jungle Trail") and 200 m (trail to Rio Jaba) of the Station grounds. Searches along stable trail and stream banks in older second growth and primary forest failed to locate any burrows. The apparent preference of these spiders for disturbed, sparsely wooded habitats is shared by *Ummidia* populations in western North Carolina (F. Coyle pers. obs.) and Arizona and Mexico (Gertsch 1979) and may be linked to a reliance on aerial dispersal by ballooning, a trait observed in populations in North Carolina (Coyle 1985; pers. obs.) and Arkansas (Baerg 1928). Such a relationship would fit Greenstone's hypothesis that less predictable habitats select for higher rates of ballooning (Greenstone 1982; Coyle et al. 1985). The type of ballooning characteristic of *Ummidia* and other mygalomorphs, ballooning which apparently requires air currents stronger than gentle updrafts (Coyle 1983, 1985), might
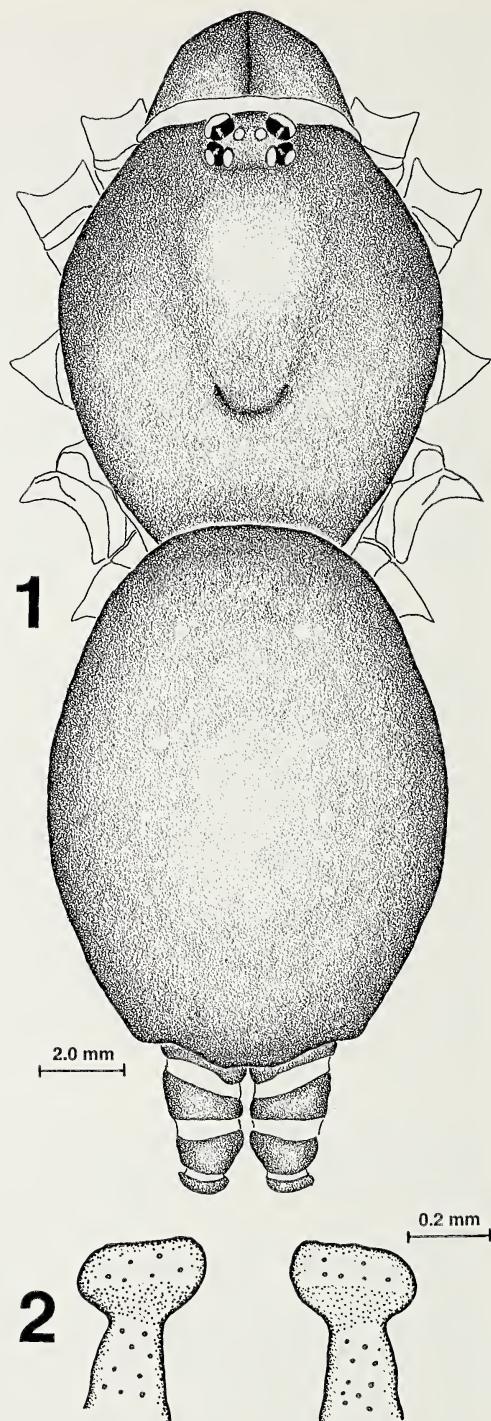
Figures 1, 2.—Adult female *Ummidia* collected in 1993 from Las Cruces, Costa Rica. 1, Dorsal view without pedipalps and legs; 2, Spermathecae.

be especially ineffective and risky for a fossorial spider living in an old growth forest, where the necessary breezes are probably rare to nonexistent except at the top of the canopy.

Despite much effort in 1993 and 1995 to find smaller burrow entrances, the great majority (94% in 1993 and 65% in 1995) were large (with door widths of 15–29 mm) and belonged to near adult or adult spiders, judging from the door widths (20–23 mm) of the three excavated burrows, all of which contained adult females. About half of these burrows were loosely clustered in groups of 2–4 burrows per m²; others were more isolated. The only smaller entrances found were one with a 10 mm wide door (1993), two with 13 mm wide doors (1995), and nine much smaller entrances of very young individuals (1995). These latter entrances were 1.5–3.5 mm wide, and all but two of these burrows were unoccupied, as evidenced by severely damaged or missing doors. Two of these very small burrows were each about 50 mm from one adult burrow, another two were 10 mm and 15 mm from another adult burrow, and the other five were between 35 mm and 180 mm from a third adult burrow. This paucity of young burrows in locations where adults are common provides additional support for the hypothesis that spiderling ballooning is the primary dispersal mode of this species. Adult female burrows of non-ballooning fossorial spiders like the antrodiaetids are often surrounded by numerous burrows of early instars (Coyle 1971; Coyle & Icenogle 1994), whereas juveniles of a North Carolina *Ummidia* population known to balloon are almost never found near an adult burrow. The higher ratio of unoccupied/occupied very small burrows (0.78) than unoccupied/occupied large burrows (0.13) found in 1995 is consistent with the expectation that young juveniles experience particularly high mortality rates because their high surface to volume ratio and shallow burrows make them especially vulnerable to environmental crises like drought and erosion.

ENTRANCE AND BURROW STRUCTURE

The trapdoor is relatively thick and rigid with beveled edges (Figs. 3, 4, 10, 11; Table 1). When the door is closed, these edges fit snugly into the tough entrance rim which flares outward to form a complementary bevel. The entrance rim is usually nearly flush with the surrounding soil but may extend as much as 5–10 mm above it. The door is composed of soil and silk. Its inner surface is covered with a thick, tough white layer of silk, and its outer surface, which is soil with bits of dead plant material and sometimes moss, resembles the surrounding ground surface (Figs. 3–5, 10–12). The door is connected to the entrance rim by a broad hinge, the bulk of which is thick tough silk continuous with the entrance rim and burrow lining. On the outer surface of some doors are roughly concentric semi-circular ridges or flaps (Figs. 3, 4) which are probably old, smaller doors to which more soil and silk were added as the spider grew. Pieces of plant material and irregular tabs of silk plus soil up to 10 mm long often extend from the entrance rim lips and door edges (Figs. 10, 11) and, like the linear litter and tabs attached to the entrances of other trapdoor spiders (Coyle 1986; Coyle et al. 1992; Coyle & Icenogle 1994), may serve to extend the spider's prey-sensing radius.

Data on burrow entrance structure is summarized in Table 1. The shape of the door is similar to that of many trapdoor taxa (Fig. 9). However, a most peculiar feature of these entrances is their orientation. Contrary to the consistently near-horizontal hinges of most other trapdoor species living on steep slopes (Coyle 1986; Coyle & Icenogle 1994), most of these *Ummidia* doors were oriented with the hinge tilted well away from the horizontal, and some were vertical or nearly so (Figs. 5, 11). In 1995, left tilting hinges (8) were less common than those tilting to the right (12).

Figures 4, 5, and 6–8 illustrate the three excavated burrows. All three extended roughly straight back (100–160 mm) into the trail bank, approximately perpendicular to the surface. As has been observed for other *Ummidia* species (Gertsch 1979), burrow diameter was fairly constant throughout each burrow's length. The full length of each burrow was lined with silk, but the silk was much thicker near the entrance than elsewhere (Figs. 4, 5). The upper third of the longest burrow was lined with an especially thick leathery lining composed of several layers of silk and soil that were probably applied in response to the very loose soil in that spot (Fig. 5).

PREY CAPTURE BEHAVIOR

The foraging posture and prey capture behavior of these spiders are similar in form to those of the North American *Ummidia* studied by Coyle (1981). Approximately 30 min after sunset the Costa Rican spiders assumed the foraging pos-
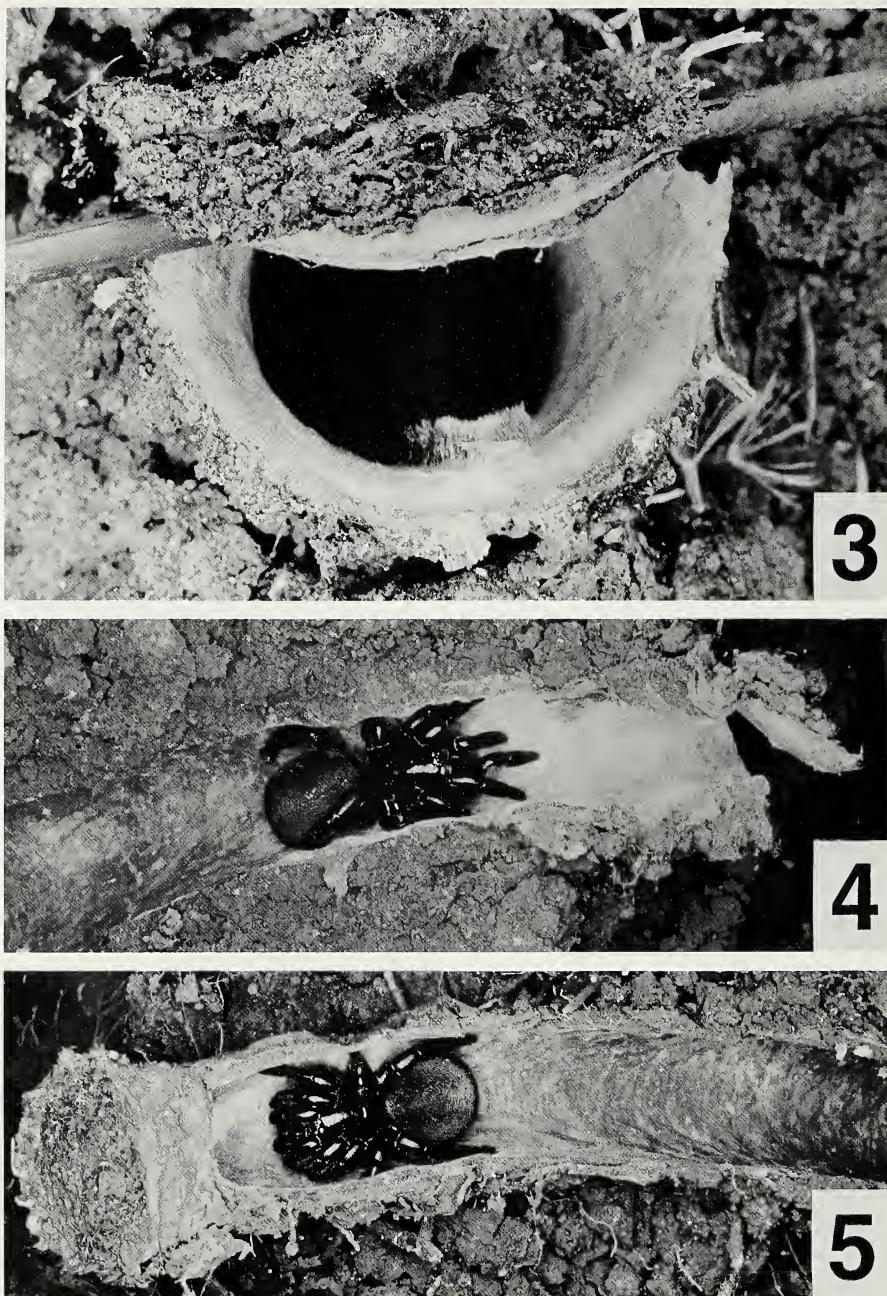
Figures 3–5.—Photos of burrows of adult females of *Ummidia* at Las Cruces, Costa Rica. 3, Entrance with trapdoor propped open to show small broken silk seal and small old door attached to upper surface of functional trapdoor; 4, Side view of burrow and trapdoor excavated (same as in Fig. 3) in 1992, with female (upper wall of upper end of burrow has collapsed so that door is shifted from its normal position); 5, Side view of burrow excavated in 1993, with female, showing nearly vertical hinge and upper surface of partly open trapdoor.

ture; the trapdoor is opened slightly (1–3 mm) and the spider is positioned just below the door with the tarsi of its pedipalps and first and second legs resting on the lip of the entrance rim (Fig.

10). Several arthropods were placed near entrances to elicit prey capture responses. Only three capture attempts were observed; an opilionid was attacked when it touched the trapdoor with one

Table 1.—Orientation, dimensions, and shape indices of *Ummidia* trapdoors from Las Cruces Field Station, Costa Rica. Range, mean, and standard deviation given. Only larger entrances (doors over 14 mm wide) included. 1995 sample ($n = 20$) was measured by Coyle and included many of the entrances in the sample ($n = 15$) measured by Bond in 1993. Door hinge index = door width/hinge width, and door shape index = door width/door height; see Fig. 9.

	1993 sample	1995 sample
Door thickness (mm)	1.5–3.0, 2.46 ± 0.57	
Hinge angle (degrees)	0–90, 51.0 ± 33.4	0–85, 40.1 ± 24.0
Hinge width (mm)	13–21, 16.9 ± 2.0	14–25, 18.7 ± 3.0
Door width (mm)	15–27, 19.3 ± 3.0	16–29, 21.6 ± 3.0
Door height (mm)		11–22, 16.9 ± 2.6
Door hinge index	1.00–1.29, 1.14 ± 0.10	1.00–1.29, 1.16 ± 0.07
Door shape index		1.13–1.47, 1.29 ± 0.09

of its tarsi, a broad caterpillar covered with white scalelike hairs was attacked when it crawled within 1–2 mm of the trapdoor, and a small hemipteran was captured when it walked within 3–5 mm of the trapdoor. In all cases the door popped open and the spider lunged from the entrance, exposing all but the posterior half of its abdomen while holding onto the burrow with its fourth and possibly third legs. Prey were grabbed with the pedipalps and first legs. The opilionid and caterpillar were immediately released, but the pedipalps and legs flexed to pull the hemipteran close to the chelicerae for the strike, after which

the spider immediately retreated into the burrow with prey.

DEFENSIVE BEHAVIOR

At night spiders were quick to pull their doors shut and hold them tightly closed when the entrances were directly illuminated by a flashlight. During daylight hours, attempts to open (with a knife blade) or measure closed doors often caused the spiders to quickly pull the doors tightly closed; clearly many spiders monitor their entrances rather closely, even in the daytime when doors are closed and substrate vibrations may be the
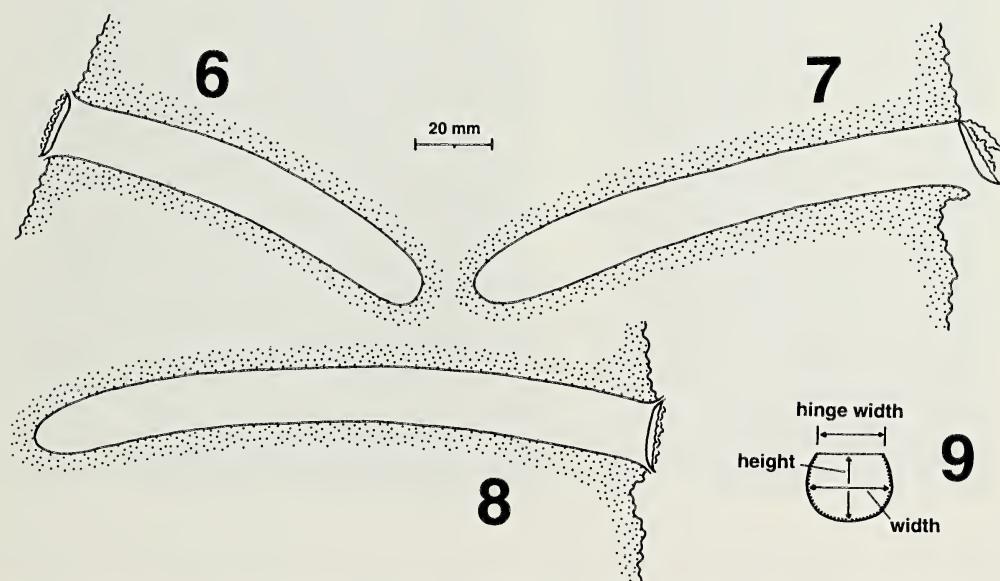
Figures 6–9.—Drawings of burrows of *Ummidia* females at Las Cruces, Costa Rica. 6–8, Side view drawings of the three adult female burrows that were excavated; 6, 1995 burrow; 7, 1992 burrow; 8, 1993 burrow; 9, Outline of trapdoor based on mean dimensions of 1995 sample and showing the three door shape measurements.
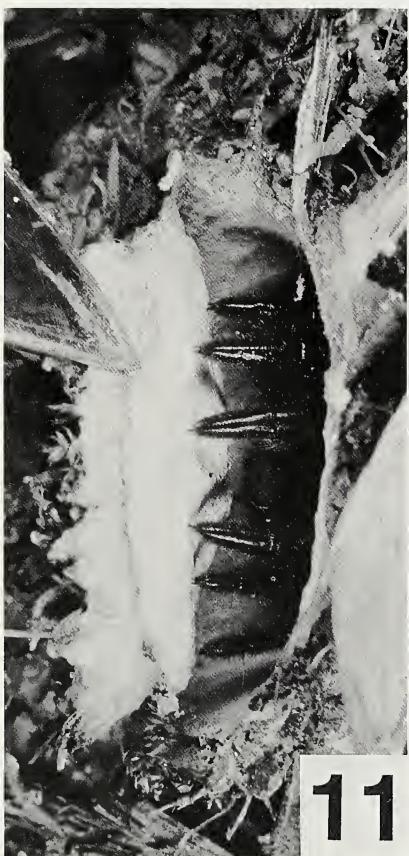
Figures 10–12.—Photos of burrow entrance behavior of adult females of *Ummidia* at Las Cruces, Costa Rica. 10, Spider in foraging posture at night; arrows point to claws, from left to right, of right leg II, right leg I, right pedipalp, left pedipalp, and left leg I touching entrance rim; 11, Spider attempting to close door with fangs and claws of pedipalps, legs I, and legs II; 12, Spider attempting to close fully opened door with claws and fangs while anchoring itself in burrow with legs III.

only sign of danger. As Gertsch (1979) observed in other *Ummidia* species, a great deal of force is required to pry open these secured trapdoors with a knife blade or pair of forceps. Even when the door is forced open the spider continues to maintain its grip, revealing its method (Figs. 11, 12). With its venter facing the hinge, the spider holds the inner surface of the door with its fangs and the claws of its pedipalps and first and second legs, much as described by Gertsch (1979) and Coyle (1981) for North American *Ummidia* species. Claw and fang marks are found on the undersurface of all doors (Fig. 12). The spider anchors itself to the burrow by pressing the enlarged distal end of the saddle-shaped tibia and adjacent dorsal surface of the metatarsus of each third leg against the burrow wall (Fig. 12), as described for North American *Ummidia* populations by Coyle (1981), and by presumably holding onto the wall deeper in the burrow with the tarsal claws of its fourth legs. By opening doors in the daytime when spiders were not in contact with their doors, we could see that a spider usually closes its door with its tarsal claws before inserting its fangs. While this mode of door-holding requires that a spider in foraging position first rotate 180° around its longitudinal axis, an extra maneuver which taxa that hold doors shut only with tarsal claws need not perform (Coyle et al. 1992), the *Ummidia* mode probably produces much more pulling power than if fangs are not used.

Two spiders, one in 1992 and one in 1995, had each lightly sealed its door shut with a thin small patch of silk (Fig. 3) but moved up and closed the door after it was forced open. These seals appeared too weak to prevent predators from forcing the doors open, and instead may serve to hold the door more tightly against the entrance lip during the daytime to reduce the evaporative loss of burrow moisture or ensure crypsis. Another spider exhibited a curious, seemingly vulnerable, posture on two successive afternoons in 1993; it was found motionless and reaching out of the burrow entrance holding onto the undersurface of a fully opened door with its fangs and pedipalp and leg claws so that its prosoma and anterior abdomen were fully exposed. Upon sensing the observer, it retreated into the burrow and pulled the door shut.

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CHIVALRY IN PHOLCID SPIDERS REVISITED

Julie A. Blanchong, Michael S. Summerfield, Mary Ann Popson, and Elizabeth M. Jakob[1]: Department of Biology, Bowling Green State University, Bowling Green, Ohio 43403 USA

ABSTRACT. Cohabiting pairs of adult spiders are likely to interact over prey, and the outcome of these interactions is likely to affect the reproductive success of both individuals. In two species of pholcid spiders, previous workers reported the occurrence of "chivalrous" behavior, in which males cede prey to females. We looked for the occurrence of chivalrous behavior in another pholcid spider, *Holocnemus pluchei*. Pairs of spiders were placed on a web and left overnight without prey. A housefly was then introduced onto the web equidistant from the spiders, and subsequent interactions were noted on audiotape. We found no evidence of chivalry in pairs of unknown mating status or in pairs that had recently mated: males and females were equally likely to win the prey, and intensity of interactions over prey was not influenced by the gender of the winner. The differences in our results compared to previously published work may be attributable to the fact that *Holocnemus* lives in unusually dense populations in nature. This, in combination with a pattern of last-male sperm priority, means that females may be difficult for males to monopolize, and a male will not substantially increase his own reproductive success by ceding prey to a female with which he has mated if others are also likely to mate with her.

Web-building spider species vary tremendously in the duration of male and female cohabitation. Spiders may interact only during courtship and copulation (Robinson 1982), live permanently in the same colony (see reviews by Buskirk 1982; D'Andrea 1987), or exhibit behavior between these extremes (Suter & Walberer 1989). While sharing a web, males and females can interact over incoming prey. These interactions also vary greatly, ranging from cooperative prey capture in some social species (Buskirk 1982), to forceful battles over prey (Suter 1985). Interactions over prey by cohabiting pairs are potentially of evolutionary importance because an increase in a female's prey intake is likely to increase her fecundity (e. g., Turnbull 1962) and cohabitation can be relatively prolonged. The extent to which a cohabiting male benefits from consuming prey himself or allowing a female to consume prey may be influenced by whether he has mated with the female, the number of other mates she has had, the pattern of sperm priority, the female's defendability, and the number of other mating opportunities in the population.

A particularly striking example of interactions over prey is the "chivalrous" behavior reported by Eberhard & Briceño (1983), in which male

pholcids ceded prey to females. *Blechroscelis* sp. males, after attacking prey, would sometimes step aside and allow a female to take it. Occasionally, a female would vibrate her abdomen (a display also seen in male courtship, and interpreted by Eberhard & Briceño as "begging"); this behavior was often followed by the male ceding the prey to her. In two *Modisimus* species, males initiated most attacks on prey and then usually ceded the prey to females. In one species, the female would approach the male as he wrapped the prey, then he would step aside and allow the female to take the prey. In the other species, males usually completely wrapped the prey, then plucked the web, and left the prey in the web for the female or carried it towards her. Eberhard & Briceño (1983) termed these behaviors "chivalrous" because males sometimes endured partial starvation while allowing females to feed, and we follow their terminology here.

We looked for the occurrence of chivalrous behavior in another pholcid spider, *Holocnemus pluchei*. Several factors make *Holocnemus* a good species in which to study this behavior. First, it serves as a comparison to the pholcids studied by Eberhard & Briceño (1983). *Holocnemus* often live in dense populations with interconnecting webs and a single sheet of silk may be shared by many spiders of all ages, in contrast to *Blechroscelis* and *Modisimus*, in which only adult pairs cohabit (Eberhard & Briceño 1985). Sec-

[1] To whom correspondence should be addressed.

ond, interactions between *Holocnemus* spiders over prey are relatively well known (Jakob 1991, 1994), allowing us to interpret clearly their behaviors. Finally, we have some information about the sperm priority pattern in *Holocnemus*. In *Holocnemus*, the second of a pair of males to mate with a female fertilizes 65–82% (95% confidence interval) of her eggs (Kaster 1995). With this information, the implications of chivalrous behavior for a male's reproductive success are more easily interpreted.

In our laboratory study, we introduced prey onto webs shared by male and female pairs of adult spiders and noted subsequent interactions, watching especially for behavior patterns described by Eberhard & Briceño (1983). We define chivalrous behavior by male spiders to include the following: (1) upon the approach of a female, the male leaves the prey and stands aside as she takes possession, (2) the male wraps and then carries the prey to or in the direction of the female and cedes it to her, or (3) both spiders simultaneously wrap the prey, and the male subsequently moves away, with little or no aggression by the female. If males are chivalrous, they might allow females to attack prey first, and females may be more likely to win interactions over prey. Chivalrous males might cede prey without escalating interactions, so we also examined the relationship between interaction intensity and the gender of the winner. We also analyzed relative frequency of other aggressive behaviors for males and females to look for any gender-specific differences. We studied two groups of spiders: pairs that may or may not have mated (with other spiders or with each other) prior to the test (mating status unknown, or MSU), and previously virgin pairs that were observed to mate with one another prior to the test.

METHODS

Adult and juvenile *Holocnemus pluchei* were collected in Davis, California in the summer of 1994 and shipped to our laboratory in Ohio. Rearing procedures follow Jakob & Dingle (1990) with the following exceptions. Juveniles were reared to maturity with three feedings per week of fruit flies (*Drosophila* sp.) and flour beetle larvae (*Tribolium confusum*). Adults were fed houseflies (*Musca domesticus*) and *Tribolium* larvae twice weekly. Spiders were maintained in a room with 16:8 L:D cycle at a temperature of approximately 27 °C.

The experimental arenas were four $52 \times 37 \times 22$ cm plastic cages. Because *Holocnemus* are slow to build large webs in the laboratory, we introduced spiders onto webs built by conspecifics. In the field, *Holocnemus* routinely use webs that other individuals have built (Jakob 1991), so this is a realistic approximation of field conditions.

We performed two sets of trials. In the first set of 31 trials (mating status unknown, or MSU), field-caught spiders were randomly paired as adults, introduced into a web and left overnight. Because we did not monitor the spiders after pairing and prior to the test, we did not know whether these pairs mated in the laboratory. In the second set of 14 trials (mated pairs), mature virgin spiders were randomly paired and introduced into a test web, where we observed copulation. Testing occurred approximately 24 hours after copulation. Within one-half hour before the start of all trials, we briefly removed spiders from the test arena without damaging the web, and weighed them on a Mettler balance. After their return to the web, spiders were given a few minutes to acclimate before testing began.

At the start of each trial, a housefly was anesthetized with CO_2 and placed in the web with soft forceps approximately equidistant from each member of the pair, which were typically within 25 cm of each other. We made continuous voice recordings of observations with a microcassette recorder, beginning when the fly first moved. We noted whether both spiders oriented to the prey (turned to face the prey), which spider was first to attack the prey, if one spider relinquished the prey without fighting, and which spider ultimately won the prey. We also noted if the prey changed possession during the course of the interaction: that is, if it was first held by one spider in its chelicerae and later by the other. Trials ended when one spider was feeding on the prey and both spiders had been quiescent for at least 10 min. Previous observations suggest that spiders rarely steal prey after feeding begins (Jakob 1991).

We classified interactions over prey into three levels after Jakob (1994). Interactions at lower levels are assumed to have lower risk of injury than interactions at higher levels. *Level I*: Orientation to conspecific (spider turns its body to face conspecific), pushups (slow leg flexion) and abdomen twitching (fast dorsal/ventral twitching of the abdomen). *Level II*: Bouncing (sharply contracting its legs so body moves toward the

Table 1.—Number of trials in which males and females won the prey item. χ^2 goodness-of-fit tests are against expected values of 50:50. Calculations of the power of the test follow Cohen (1977).

	Male won	Female won	χ^2	P	Power
Mating status unknown	10	16	1.397	0.391	0.507
Mated pairs	9	5	1.143	0.428	0.513
All trials	19	21	0.100	0.752	0.764

web), approach conspecific, and web plucking (spider spreads its anterior pair of legs, pulls sharply downward on the web, and releases it so the silk snaps back). *Level III:* Chasing a conspecific, probing and contacting the conspecific with extended front legs, and grappling (locking chelicerae, intertwining legs and appearing to roll about the underside of the web sheet). From tape transcriptions, we calculated interaction time, excluding pauses between activities, for behaviors of all levels combined and for behaviors of Levels II and III only.

For results reported here, we omitted trials in which one of the spiders failed to respond to the prey at any time because we did not know if spiders had detected the vibrations of the prey. In MSU pairs, three males failed to respond to the prey at any time throughout the trial and two females failed to respond. In trials with mated pairs, the male did not respond in one trial and the female did not respond in another. Inclusion of these trials did not change the outcome of the analyses.

We compared the frequencies that males and females attacked and captured prey against expected frequencies of 50% with χ^2 goodness-of-fit tests. We used contingency tests to examine differences in the levels of escalation of interactions when males and females won. Contingency tables were analyzed with G-tests when cell sample sizes permitted and with χ^2 contingency analyses for other cases (Sokal & Rohlf 1981). We used nonparametric tests to examine whether

interactions won by males were of the same duration as those won by females.

RESULTS

General descriptions of interactions.—Males and females were equally likely to attack the prey: in all trials combined, 20 females were first to attack the prey and 20 males were first to attack. MSU and mated trials did not differ significantly: in MSU pairs, 11 males and 15 females were first to attack, and in mated pairs, 9 males and 5 females were first (contingency table, $G^2 = 1.777$, $P > 0.15$). There were competitive interactions over prey in every trial, and every trial ended with one spider feeding on the prey.

Winner of the interaction.—If males were chivalrous, females would be expected to win interactions over prey more often than males. However, males and females were equally likely to win the prey (Table 1). Mated and MSU pairs did not differ significantly (contingency table, $G^2 = 2.456$, $df = 1$, $P > 0.12$).

We were interested in the combined effects of relative mass and prey on the outcome of interactions: chivalry might be occurring if males lost prey to females of smaller mass. This effect might be hidden in the data because, as a group, *Holocnemus* males were significantly lighter than females with which they were paired (Wilcoxon signed-rank test, $Z = -3.737$, $P = 0.0002$). We categorized males as being within 10% of the mass of their partner (hereafter classified as same size), less than 10% of the female's mass (smaller males), or greater than 10% of the female's mass (larger males) (Table 2). Smaller males lost more interactions than expected, but this difference was not significant (contingency table, $G^2 = 5.474$, $df = 2$, $0.06 < P < 0.07$). When we pooled same size and larger males, we found that they were significantly more likely to win fights over prey than were smaller (contingency table, $G^2 = 5.357$, $df = 1$, $P < 0.03$). Thus, contrary to predictions from chivalry, males tended to lose in-

Table 2.—Number of males and females that won the prey item for three relative weight classes.

	Larger males	Male within 10% of female	Smaller males
Male	5	4	10
Female	2	1	18

Table 3.—Level of interactions reached by pairs of spiders. Higher interaction levels are considered to be of higher energetic cost and higher risk.

	Level I	Level II	Level III
Mating status unknown			
Male wins	1	4	5
Female wins	0	5	11
Mated pairs			
Male wins	2	1	6
Female wins	0	0	5

teractions only when they were smaller than their partners.

Interaction intensity.—Chivalry might occur in a more subtle way: perhaps males gave up prey without escalating interactions to their highest level. For all trials combined, three interactions did not pass beyond Level I, 10 did not pass beyond Level II, and 27 reached Level III, the highest intensity level. There was no relationship between the level of intensity that interactions reached and the gender of the winner for MSU pairs ($x^2 = 2.088$, $df = 2$, $P > 0.35$), mated pairs ($x^2 = 2.121$, $df = 2$, $P > 0.3$), or all trials combined ($x^2 = 3.836$, $df = 2$, $P > 0.14$) (Table 3). MSU and mated pairs did not differ significantly in the level of interaction that was reached. No relationship was found between relative masses of a pair (male within 10% of its partner's mass, less than 10%, or greater than 10%) and interaction intensity ($x^2 = 1.744$, $df = 2$, $P > 0.78$).

Change of possession of the prey.—If chivalry occurs in this species, we would predict that prey would more often change from the possession of the male to the possession of the female. In five MSU pairs, the prey changed possession during the course of the interaction. In three trials, the prey was taken away from the male by the female, and in two trials, the prey was taken away from the female by the male. In mated pairs, the prey changed possession from the male to the female once, and on one occasion, the prey changed from the female, to the male, then back to the female, who consumed it.

Behavior.—No spider ever stood aside as another took the prey, wrapped the prey and then ceded it without aggression, or simultaneously wrapped the prey with another spider and then moved away.

We also looked for more subtle evidence of chivalry by investigating whether females and males differed in their performance of specific agonistic behaviors. We counted the number of trials in which each behavior was performed at least once by the male or female. We found no significant differences in pushups, bouncing, approach, chasing, web plucking or probing. However, the numbers of trials in which the male abdomen twitched was significantly higher than the number of trials in which the female abdomen twitched (contingency table analysis, male: 32 of 40 (60%); female: 14 of 40 (35%); $G^2 = 17.269$, $df = 1$, $P < 0.0001$).

Interaction duration.—If chivalrous males give up prey to females, interactions that are won by females may be shorter in duration. However, we found no significant relationship between gender of the winner and duration of all interactions (excluding pauses) or for duration of all behaviors of level II or III (Mann-Whitney U-tests) (Table 4). When MSU and mated pairs were analyzed separately, no significant difference in any measure of duration was found.

DISCUSSION

Holocnemus pluchei were not chivalrous. Males and females were equally likely to attack and win prey. However, the power of our test comparing the frequency of winning for each gender (Table 1) indicates that we have a 24% probability of a Type II error, or accepting the null hypothesis when it is false; thus, this result alone does not

Table 4.—Mean (±SE) interaction durations (s) in trials that females won compared to trials that males won. P values are derived from Mann-Whitney U-tests.

	Duration of all interaction levels			Duration of II & III		
	Female won	Male won	P	Female won	Male won	P
Mating status unknown	543 ± 134	492 ± 126	NS	193 ± 76	110 ± 36	NS
Mated	932 ± 312	257 ± 76	0.10	389 ± 186	79 ± 27	0.10
All trials	636 ± 128	381 ± 78	NS	171 ± 41	239 ± 73	NS

firmly establish that these spiders are not chivalrous. However, we saw none of the chivalrous behaviors described by Eberhard & Briceño (1983). Fights over prey often escalated. Prey changed hands from male to female approximately as often as it changed from female to male. Males that were within 10% of the body mass of females or larger than females were likely to win prey, suggesting that when males lose prey, it is not because of chivalry but because of a lack of competitive ability. Few differences were found in male and female behavior patterns. Males were more likely to abdomen twitch; the meaning of this behavior is unclear, but we interpret it as a low-risk, low energy behavior. In sum, we found no evidence that males were allowing females an advantage in prey capture.

Eberhard & Briceño (1983) suggest that, for *Blechroscelis* and *Modisimus*, it is to a male's advantage to be chivalrous if it results in an increase in the number of eggs laid by the female that are sired by the male. Although mating was not directly observed in Eberhard & Briceño's (1983) study, it is likely that their spiders had mated; only adult pairs cohabit, and paired males will fight with males that are introduced onto the web (Eberhard & Briceño 1985), which is consistent with the idea that females are a valuable resource worthy of defense (e. g., Parker 1984). The last pholcid male to mate with a female may father many of her eggs: Austad (1984) predicts that, based on the cul-de-sac shape of the spermatheca, haplogyne spiders such as pholcids should show last male sperm priority or sperm mixing. Eberhard et al. (1993) found that in another pholcid, *Physocyclus globosus*, sperm priority pattern for twelve females that were each mated with two males did not differ from that expected for random sperm mixing. If Austad's prediction proves true for *Blechroscelis* and *Modisimus*, it should benefit a male to cede prey to a female with which he has just mated.

Why, then, are *Holocnemus* males not chivalrous? Kaster (1995) found, using the technique of sterilization by irradiation, that the sperm priority pattern in *Holocnemus* is highly variable: the second male of a pair of males fertilized between 2.6 and 100% of a female's eggs. High variability in sperm precedence is common in insects and is as yet unexplained (Lewis & Austad 1990). However, in most of Kaster's pairs of males, the second male fathered most of the eggs ($\bar{x}$ = 73.7%, 95% confidence interval 65.8–81.6%).

It seems clear that the first male to mate with a virgin female is not guaranteed to fertilize the bulk of her eggs if the female has subsequent mates. A male that cedes prey to a female may not gain much benefit in reproductive success if another male mates after he does.

Holocnemus differs from the species that Eberhard & Briceño studied in that *Holocnemus* females may not be a defendable resource. *Holocnemus* populations are extremely dense: for example, there may be over 600 spiders on a 3 m × 15 m juniper bush (Jakob unpubl. data). Both males and females move frequently from one web to another (Jakob 1991), so the intrusion rate of potential competitors for a female's attentions and the rate of female encounters with new males are both likely to be high. In the laboratory, females readily remate: Kaster (1995) removed males when they finished copulating with a virgin female and immediately introduced a new male, and found that copulation began again in an average of 437 sec (SE = 101.91, n = 20). The populations of *Blechroscelis* and *Modisimus* are less dense than those of *Holocnemus*, and webs of individuals or pairs are discrete (W. G. Eberhard pers. comm.). Male *Blechroscelis* and *Modisimus* are more likely to be able to successfully defend females from competitors. An additional effect of the high population density of *Holocnemus* is that males are likely to have other mating opportunities, which would devalue any one mating and make it profitable for a male to increase its energetic intake to allow further searching for mates. Other variables that would affect a male's probability of finding more than one mate include predation risk while searching and the male's expected lifespan. Neither of these, to our knowledge, has been measured for any pholcid in the field. However, *Holocnemus* males can live for over a year in the laboratory (unpubl. data), which suggests they may indeed have ample opportunity to remate in the field.

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GENERIC PLACEMENT OF THE EMPIRE CAVE PSEUDOSCORPION, *MICROCREAGRIS IMPERIALIS* (NEOBISIIDAE), A POTENTIALLY ENDANGERED ARACHNID

William B. Muchmore: Department of Biology, University of Rochester, Rochester, New York 14627 USA

James C. Cokendolpher: Adjunct Professor, Department of Biology, Midwestern State University, Wichita Falls, Texas 76308 USA

ABSTRACT. Types, topotypes, and some other material of the pseudoscorpion *Microcreagris imperialis* Muchmore have been studied, and the species is transferred to the genus *Fissilicreagris* Ćurčić. Supplemental description and illustrations are presented, including the first information about females. This species is known only from three caves in Cave Gulch, Santa Cruz County, California. The cave habitat for *F. imperialis* is threatened by vandalism, development, and closure; and the U. S. Fish and Wildlife Service has proposed this pseudoscorpion as a candidate for listing as an endangered or threatened species.

More than 1500 species and subspecies of animals in the United States are proposed by the U. S. Fish and Wildlife Service for listing as endangered or threatened (Drewry 1994). In most instances, these taxa have been submitted for consideration in the absence of any validation of taxonomic status. One of the candidate species of pseudoscorpions being reviewed for possible addition to the List of Endangered and Threatened Wildlife under the Endangered Species Act of 1973, as emended, is *Microcreagris imperialis* Muchmore, from Empire Cave, Santa Cruz County, California.

As Mahnert (1979) and Ćurčić (1983) have demonstrated, the genus *Microcreagris* Balzan is restricted to two species in China and Afghanistan, and the numerous American species which had been placed in that genus are improperly assigned. Ćurčić (1978–1989) created quite a few new genera and placed many of the American species in them; he was, however, unable to make definite generic assignments for some species, including *M. imperialis* (1984:165).

The purpose of this paper is to clarify the taxonomic position of *M. imperialis* so that this potentially endangered species can be identified properly in the literature. Furthermore, we wish to provide sufficient identification characteristics so that field biologists might more easily recognize this species in its native habitat.

METHODS

Specimens have been borrowed from the American Museum of Natural History, New York, New York (AMNH); California Academy of Sciences, San Francisco, California (CAS); D. Ubick personal collection, San Francisco, California (CDU); and the Florida State Collection of Arthropods, Gainesville, Florida (FSCA).

Unless otherwise stated, the specimens have been dissected, cleared, and mounted in Canada balsam on microscope slides.

Fissilicreagris imperialis (Muchmore),
new combination
Empire Cave Pseudoscorpion
Figs. 1–9

Microcreagris imperialis Muchmore 1969:13–15, 21, fig. 10; Arnett 1984:21666; Briggs & Ubick 1988:44; Drewry 1989:566; Coddington, Larcher & Cokendolpher 1990:11; Drewry 1991:58833; Harvey 1991: 342; Drewry 1994:59025.
'*Microcreagris*' *imperialis*: Ćurčić 1984:164, 165, figs. 20, 41.
Pseudoscorpion: Briggs 1990:180.

Type locality.—Empire Cave, in Cave Gulch, one mile NW of Santa Cruz, Santa Cruz County, California.

Material examined.—Holotype male and one paratype male from Empire Cave, 26 August
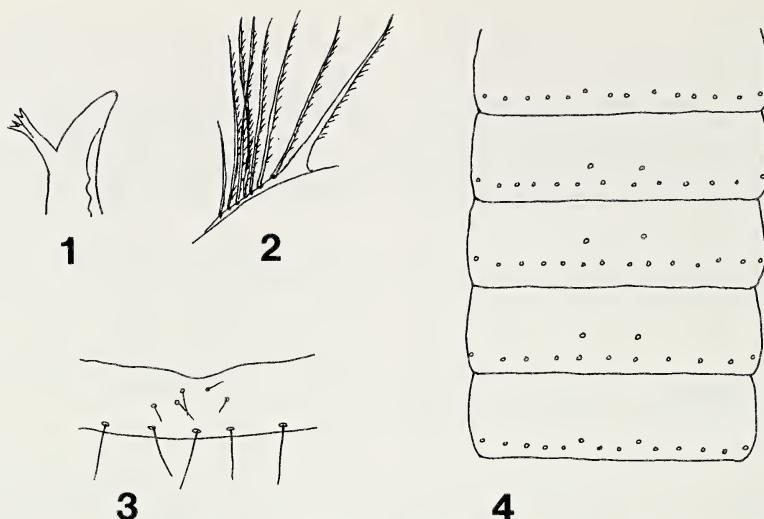
Figures 1–4. — *Fissilicreagris imperialis* (Muchmore), male holotype. 1, Tip of movable finger of chelicera, with galea; 2, Cheliceral flagellum; 3, Central part of sternite 3; 4, Sternites 5–9, showing chaetotaxy (setae omitted).

1963, R. E. Graham, mounted on slides (AMNH); one paratype male, same data (FSCA); one topotype female from Empire Cave, September 1972, R. Lem, mounted on slide (CAS); one topotype male from Empire Cave, 8 July 1989, D. Ubick, et al., in alcohol (CDU); two topotype males from Empire Cave, 8 September 1991, D. Ubick and S. Fend, mounted on slides (CAS); one female from Dolloff Cave, across Cave Gulch from Empire Cave, 22 April 1979, D. C. Rudolph et al., mounted on slide (CAS); three females from IXL Cave, in Cave Gulch one-half mile S of Dolloff Cave, 21 April 1979, D. C. Rudolph et al., two mounted, one in alcohol (CAS).

Supplementary description. — The topotypes and specimens from Dolloff and IXL caves are generally similar to the holotype and paratypes. Dimensions, proportions, and chaetotaxies of body and appendages vary slightly from the values given in the original description, but all appear conspecific with the types. A few features of the additional specimens are, however, worth mentioning.

Apex of palpal coxa (manducatory process) bears three setae in all specimens, as in types. Cheliceral galea short and twice bifid (Fig. 1); galeae of types also like this, not just "with four or five terminal spinules" as characterized in original description (Muchmore 1969:15). Cheliceral flagellum composed of 7–8 serrate setae (Fig. 2). Sternites 6, 7, and 8 with two setae on face near middle (discal setae) as in types (one

topotype with two setae on face of sternite 5); sternites 9 and 10 with two corresponding setae slightly anterior to the marginal row (Fig. 4). Trichobothria on palpal chela of holotype as shown in Fig. 5 (and Ćurčić 1984: fig. 41); there is a little variation in position of trichobothria on fixed fingers of other specimens (Fig. 6). Genital opercula (sternites 2 and 3) of male about as illustrated for holotype (Ćurčić 1984: fig. 20); sternite 3 of holotype with 22 setae scattered broadly (paratypes and topotypes with 18–22 setae); sternite 3 of holotype with five small setae near middle and 11 larger setae along posterior margin (paratypes and topotypes with 5–9 small setae near middle and 12–13 along margin); anterior margin of sternite 3 slightly concave at middle (Fig. 3), but not as distinctly indented as in *Fissilicreagris chamberlini* (Beier) (see Ćurčić 1984: fig. 3). Genital opercula of female as shown in Fig. 8, similar to those of *F. chamberlini* (see Ćurčić 1984: fig. 4); sternite 2 with 8–11 small setae in two groups, on either side of midline; sternite 3 with 11–14 setae along posterior margin. In both sexes, on sternites 3 and 4, there are 4–7 small setae on each spiracular plate. Internal genitalia of holotype male shown in Fig. 7; generally similar to those of *Saetigerocreagris phyllisae* (Chamberlin) (see Chamberlin 1962: fig. 12), *Tartarocreagris texana* (Muchmore) (see Muchmore 1992: fig. 4), and *Fissilicreagris macilenta* (Simon) (see Muchmore 1994: fig. 4); the dorsal sacs are thin-walled and not as clearly separate
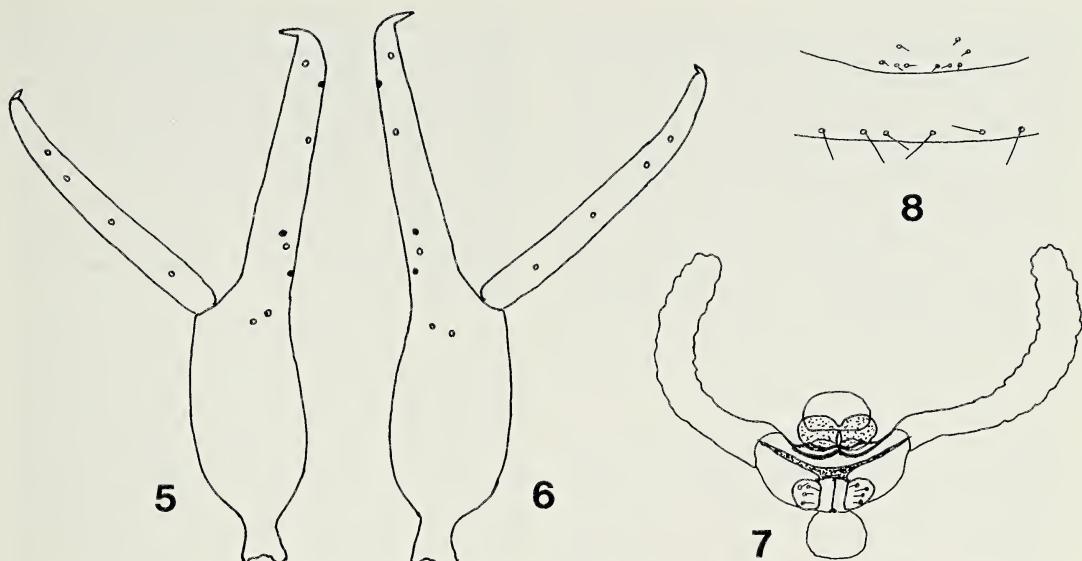
Figures 5–8.—*Fissilicreagris imperialis* (Muchmore). 5, Left palpal chela of holotype (male), lateral view, showing positions of trichobothria (darkened areoles are underneath); 6, Right palpal chela of paratype (male), lateral view; 7, Internal genitalia of holotype (male), ventral view (dorsal genital sacs stippled); 8, Central parts of sternites 2 and 3 of female (IXL Cave).
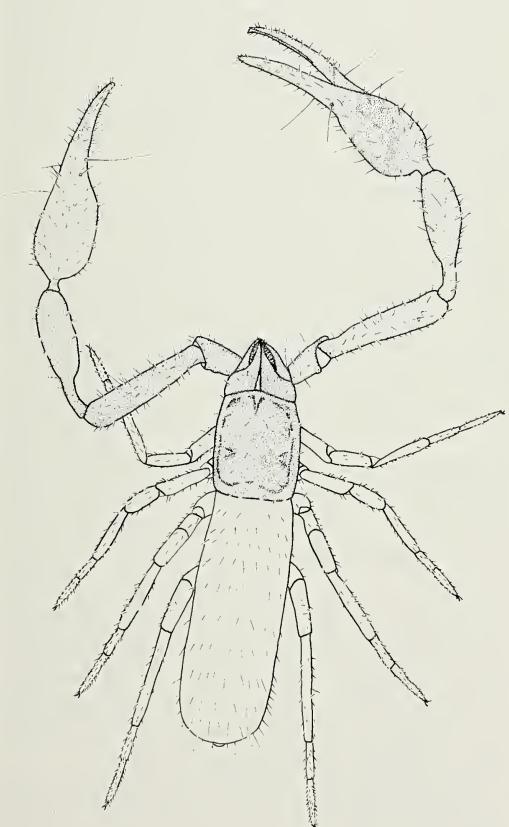
as in the three species mentioned; lateral sacs long and narrow. Internal genitalia of female not distinguished.

Measurements (mm).—*Male:* Figures given first for holotype, followed in parentheses by ranges for the two paratypes and two topotypes. Body L 3.50 (2.50–3.45). Carapace L 0.935 (0.89–0.96). Chelicera L 0.52 (0.495–0.56). Palp: trochanter 0.58 (0.56-0.63)/0.215 (0.205–0.23); femur 1.12 (1.08–1.19)/0.23 (0.215–0.24); patella 1.07 (1.00–1.11)/0.29 (0.28–0.305); chela (without pedicel) 1.73 (1.69–1.86)/0.435 (0.43–0.47); hand (without pedicel) 0.73 (0.70–0.815)/0.385 (0.38–0.43); pedicel L 0.16 (0.16–0.18); movable finger L 1.05 (1.03–1.15). Leg IV: femur + patella 0.89 (0.81–0.92)/0.215 (0.205–0.23); tibia 0.835 (0.79–0.89)/0.115 (0.11–0.125); basitarsus 0.29 (0.295–0.31)/0.095 (0.08–0.095); telotarsus 0.43 (0.40–0.445)/0.07 (0.07–0.075).

Female: Figures given first for topotype, followed in parentheses by ranges for three speci-

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Figure 9.—*Fissilicreagris imperialis* (Muchmore), female (IXL Cave). Dorsal view (setae are transparent and can only been seen with a microscope, not visible in field examinations).

mens from Dolloff and IXL caves. Body L 3.33 (3.52–3.62). Carapace L 0.89 (1.00–1.05). Chelicera L 0.525 (0.53–0.585). Palp: trochanter 0.55 (0.59–0.63)/0.215 (0.22–0.26); femur 1.03 (1.09–1.21)/0.215 (0.24–0.26); patella 0.95 (1.03–1.14)/0.265 (0.29–0.325); chela (without pedicel) 1.67 (1.76–1.91)/0.43 (0.48–0.55); hand (without pedicel) 0.70 (0.76–0.87)/0.385 (0.43–0.50); pedicel L 0.15 (0.17–0.20); movable finger L 0.96 (1.04–1.16). Leg IV: femur + patella 0.79 (0.87–0.96)/0.18 (0.21–0.235); tibia 0.74 (0.85–0.925)/0.11 (0.12–0.125); basitarsus 0.27 (0.30–0.32)/0.08 (0.09–0.105); telotarsus 0.39 (0.415–0.445)/0.075 (0.08).

Remarks.—Attempting to place *M. imperialis* in a genus, Ćurčić (1984:165) stated "In most of its diagnostic characters (shape of flagellum, presence of anterior discal setae on abdominal sternites, chaetotaxy of manducatory process, and trichobothriotaxy), it is closest to the genus *Australinocreagris* Ćurčić 1984]." This is generally correct, but it is also true that in these same characters *M. imperialis* is very similar to representatives of the genus *Fissilicreagris*, which are found in the same general area of California (see Ćurčić 1984:154–156; Muchmore 1994:63–64). In addition, the internal genitalia of male *M. imperialis* are more like those of *F. macilenta* (see Muchmore 1994) and *F. chamberlini* than those of *Australinocreagris grahami* (Muchmore) (unpubl. obs.); in particular, the dorsal genital sac of the latter species is entire and round in outline, while that of the first two species and *M. imperialis* is bilobed or divided into two separate round sacs. *Microcreagris imperialis* is also similar to the two species of the genus *Saetigerocreagris* Ćurčić in respect to the male genitalia, but it differs from them in proportions of body and appendages and in the chaetotaxies of various parts. Its relation to the genus *Tartarocreagris*, which also has similar male genitalia, but is presently known only from Texas, is uncertain.

It is concluded that *Microcreagris imperialis* Muchmore is most similar to *Fissilicreagris macilenta* and *F. chamberlini* and should be considered congeneric with them. Its major difference from them is its lack of eyes, a condition which is presumably an adaptation to life in caves.

Field recognition.—Although preserved material is required for positive identification, persons conducting a census of cave faunas or other work associated with protection of this species can be fairly certain that they have *Fissilicreagris imperialis* if: (1) it is in a cave in Cave Gulch,

and (2) it appears like Fig. 9, eyeless, and about 3.0–3.5 mm in length. The only other pseudoscorpion known from Cave Gulch is an undescribed, blind species of *Neochthonius* Chamberlin (Chthoniidae) in Empire Cave (unpubl. obs.); this is easily distinguished from *F. imperialis* by its much smaller size (only one-third as long as the latter). There are other species undoubtedly present at surface locations, but these should have eyes.

DISCUSSION

Fissilicreagris imperialis is known only from Empire, Dolloff, and IXL caves in Cave Gulch, Santa Cruz County, California. It may occur in one or more of the other caves in Cave Gulch, but it is certainly restricted to this small, isolated karst area. The three caves are all within one-half mile of each other. In addition to the new records listed under specimens examined, it is important to note that D. Ubick (pers. comm. 1995) observed but did not collect more than six specimens in Empire Cave on 3 July 1993.

Microcreagris imperialis was first listed by the U.S. Fish and Wildlife Service as a candidate for review as an endangered or threatened species over a decade ago (Arnett 1984). It is still only a candidate species and therefore it receives no substantive or procedural protection under the Endangered Species Act. Drewry (1989, 1991, 1994) continued to list this species, without a change in its status of review.

The history of Empire Cave is a tragic one. It has been known and vandalized for over 120 years (Halliday 1962). According to Graham (1967), during August 1962 the entrance to the cave was capped by a cement barrier through which a small portal (about one meter square) allowed access to the cave. This change in the entrance greatly decreased the available light in the entrance and presumably restricted air flow and increased humidity. By August 1963, a dramatic shift was noted in the distribution of cave arthropods and gastropods (Graham 1967, 1968a). Presumably the restricted entrance also altered the energy input into the cave. Graham (1968a) also noted that in 1966 the cave was blackened and filled with a strong odor, possibly gasoline. He further stated that this is the most heavily vandalized cave in the state. Despite repeated attempts to seal the cave, it has been dug open in each case (Graham 1968a).

Adamson (1982) referred to the caves in Cave Gulch as small, badly vandalized, and often lit-

tered and trashed caves. She went on to report on a clean-up trip to the caves (including Empire and Dolloff caves) during March of 1982. At that time Empire Cave was "really filled with trash including papers, wood, cigarette butts, orange peels, etc. and most dangerous, the shards of many a beer bottle. This poor cave is reputedly used for parties etc. by UCSC students." As in so many efforts to clean caves, apparently no attention was given to the fauna and how this "trash" may be affecting them. While some of the collections of this pseudoscorpion have been taken from the undersides of rocks (D. Ubick pers. comm. 1995), most specimens thus far reported from Empire Cave have been taken on wood in the cave. How many pseudoscorpions or their prey items were accidentally removed with the wood during the 1982 clean-up? It is hoped that future efforts will be better guided.

Briggs & Ubick (1988) stated that Cave Gulch on the Gray Whale Ranch and nearby Empire Cave were in danger. At that time there were plans to log the area. Those authors felt that this activity could collapse caves and disturb root systems on which primary consumers feed, alter drainage, and block entrances. If the areas were logged it could also lead to further development. Briggs (1990) continued to state that the cave habitat for this species was threatened by development and closure. A Timber Harvest Plan to log the Gray Whale Ranch and an adjacent area on Empire Grade was approved in late 1994 by the California Department of Forestry (Anonymous 1995). According to the plan, harvesting can start at anytime. The owner of the ranch has stated that the entire ranch will be logged within four years (Anonymous 1995).

Little data on the biology of pseudoscorpions in Cave Gulch caves are available. The topotype female reported herein from Empire Cave was taken under wood at 20 °C on 25 September 1972. The type series was collected "about middle of twilight zone. Each captured on the floor either on side or bottom of wood, or in one case traveling over dripstone on floor. Temp. 53.5 °F, air saturated, floor very damp." (Muchmore 1969). There are a few other observations available on the habitat, but nothing specific to the pseudoscorpion. These caves are in limestone (Graham 1966). The Cave Gulch is subject to intermittent flooding. During heavy flooding, almost all of the 75 m of Empire Cave fills with water (Halliday 1962). Dolloff Cave's entrance is almost at the level of an intermittent side stream

and must be re-excavated after every major flood (Halliday 1962). The lower portion of Empire Cave has clay floors (Graham 1967). Graham (1967, 1968a, 1968b) provided maps to Empire Cave and recorded the conditions: 29 January 1960 (6.9–7.3 °C, 94–99% R. H.), 7 August 1962 (9.0–9.3 and 12 °C, 100% R. H.), 26 August 1963 (9.3–10.9 and 12.8 °C, 96–100% R. H.). In the same publications, he also recorded the Dolloff Cave conditions as: 28 August 1963 (8.6–10.2 and 12.6 °C, 90% R. H.), 16 October 1966 (16 °C, 85% R. H.).

ACKNOWLEDGMENTS

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PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF THE SPIDER GENUS *LUTICA* (ARANEAE, ZODARIIDAE)

Martin G. Ramirez: Department of Biology, Bucknell University, Lewisburg, Pennsylvania 17837 USA

Richard D. Beckwitt: Department of Biology, Framingham State College, Framingham, Massachusetts 01701 USA

ABSTRACT. Spiders of the genus *Lutica* from 19 populations in southern California and Baja California, including all the California Channel Islands except Anacapa, were compared electrophoretically on the basis of variability at 15 gene loci. Fixed allelic differences clearly define two species: new species A [Santa Barbara and Ventura Counties, northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz), southern Channel Islands (San Nicolas, Santa Barbara, Santa Catalina)] and new species C [Guerrero Negro, central Baja California], while morphological features define two others: new species B [Los Angeles, Orange and San Diego Counties, northern Baja California] and *clementea* [San Clemente Island]. Phylogenetic analysis of the electrophoretic data using a variety of methods revealed that evolutionary rates among the populations sampled have been very unequal. The phylogenetic relationships among populations consistently supported by the electrophoretic cladograms generally correspond with the geological history of the Channel Islands and adjacent mainland and suggest certain likely colonization events involving some of the islands.

Genetic similarities and differences among populations can be used to assess specific hypotheses about biogeography and evolution. Populations on islands are especially useful because they frequently are discrete entities with little gene flow among islands; for some islands the geologic history also is known. This type of analysis is especially powerful for sedentary species in which chances for dispersal among populations are minimal (Carlquist 1981).

The California Channel Islands are an excellent system for addressing questions of evolutionary and biogeographic history. These eight islands vary in size, topography and physical isolation (Fig. 1). While the geologic history of the islands and their surroundings is complex, it has clearly involved the northward transport of these island landmasses on crustal blocks (terranes) caught in the tectonics of the Pacific/North American plate margin (Hornafius et al. 1986). It has also involved extensive changes in sea level which have repeatedly submerged some islands while possibly leaving the highest areas of others continuously above water since the Oligocene (Vedder & Howell 1980; Haq et al. 1987). Biogeographic studies of biologically old taxa on the Channel Islands need to consider both vicariance

and dispersal as factors in producing contemporary distributional patterns.

The spider family Zodariidae and many of its genera have existed since at least the Oligocene (Petrunkevitch 1942, 1952) and they have been exposed to the geological and climatic changes of the last 30 million years. Worldwide, 47 genera have been described, mainly from the tropical and temperate regions of the Old World (Jocqué 1991). Spiders of the genus *Lutica* are the only native representatives of the Zodariidae in the continental United States and they live in restricted insular and coastal dune communities in southern California and Baja California, including all the California Channel Islands except Anacapa (Ramirez 1995). Their preferred habitat is a sand dune covered by native beach vegetation located well behind the high tide line and the influence of sea water (Gertsch 1961; Ramirez 1995). On Santa Barbara Island, typical coastal dunes do not exist and these spiders live in the sandy soil and debris below vegetation growing on a sea cliff (Ramirez 1995). They live in silk-lined burrows they construct in the sand, emerging only at night to feed and, during August–October, to mate (Gertsch 1961; Ramirez 1995). When dislodged from their burrows, these

Figure 1.—Map of southern California and Baja California, including Channel Islands, showing *Lutica* sample sites. Population abbreviations follow Table 1.

spiders actively burrow into the loose sand and are quickly lost from sight. *Lutica* does not use ballooning (aerial transport on wind blown silk threads) as a means of dispersal at any point in its life cycle; ballooning is rare in other fossorial spiders (Decae 1987) and has never been recorded in the family Zodariidae (Jocqué 1993). Non-reproductive terrestrial dispersal may be minimal (Ramirez 1995). Males wandering in search of females can be found in great numbers in September; how far they actually range is not known. *Lutica* is thought to have a lifespan of two to three years (Gertsch 1961; W. Icenogle pers. comm.).

In this study, we present the results of a survey of allozyme variation among *Lutica* populations from the Channel Islands and mainland of southern California and Baja California. The primary objective was to use allozyme variation to identify valid species of *Lutica* and to determine their phylogenetic relationships. A second objective was to use the phylogenetic relationships indicated by the electrophoretic data to discuss the historical biogeography of this genus, with particular attention to estimating probable patterns

of colonization among island and mainland populations.

METHODS

Systematic background.—George Marx first described the genus *Lutica* from Klamath Lake, Oregon (Marx 1891). Gertsch (1961) corrected the type locality of *Lutica maculata* to Santa Rosa Island, California, and also described three new species: *nicolasia* (San Nicolas Island), *clementea* (San Clemente Island) and *abalonea* (Oxnard, Ventura County). Additional species have been described from India (Tikader 1981), but these taxa are clearly misplaced (Jocqué 1991).

Collections.—During 1985 and 1987, we collected *Lutica* from 19 sites in southern California and Baja California, covering a range of 865 km (Fig. 1). Sample sizes ranged from 20–50 spiders per population for a total of 812 spiders (Table 1). In the laboratory, they were starved for at least a week and then frozen at −70 °C until they were prepared for electrophoresis.

Electrophoresis.—A survey of 60 enzymes on 2–7 buffer systems revealed consistently scorable activity for 15 loci on three buffer systems; electrophoretic techniques and staining protocols are described in Ramirez (1990). No significant differences in the banding patterns of spiders of different ages or sex were ever detected, making it possible to examine spiders of all instars. All genotypes were inferred from the appearance of the staining patterns and the known subunit structure of the enzymes (Harris & Hopkinson 1976; Richardson et al. 1986).

Species identification.—In this study, the detection of fixed allelic differences was the criterion for species identification, in accord with the biological species concept [i.e., a fixed difference reflects the separate gene pools of two non-interbreeding taxa (Mayr 1970)] and following the recommendations of Farris (1981) and Richardson et al. (1986). Since it has been shown that a sample of three individuals each from two different populations is sufficient to reveal a fixed allelic difference between the populations (Richardson et al. 1986), the mean sample sizes per locus in this study, which ranged from 33–46 for 16 populations and 19–22 for three populations, were certainly adequate for the detection of fixed differences and the identification of species. In cases where diagnostic loci could not be found for a group of populations, reference was made to the morphological taxonomy of Gertsch (1961, pers. comm.) for evidence that might suggest val-

Table 1.—Summary of collections of *Lutica*. Samples include spiders of all instars.

Locality (abbreviation)	Sample size	Dates of sampling
Coal Oil Point Reserve (COP) (Santa Barbara County)	48	May 12, 1985
McGrath State Beach (MG) (Ventura County)	48	June 11 & August 15, 1985
Oxnard Beach (OX) (Ventura County)	36	June 11, 1985
La Jolla Beach (LJB) (Ventura County)	48	May 27, 1985
San Miguel Island (SMI) Cuyler Harbor	48	August 13, 1985
Santa Rosa Island (SRI) Southeast Anchorage	48	July 1, 1987
Santa Cruz Island (SCI) Johnstons Lee	48	August 17, 1985
Santa Barbara Island (SBI) Cliffs south of Signal Peak	48	July 9–10, 1987
San Nicolas Island		
Army Camp Beach (SNA)	24	July 31, 1985
Dutch Harbor (SND)	22	July 30, 1985
Red Eye Beach (SNE)	20	July 31, 1985
Santa Catalina Island (CAT) Little Harbor	48	August 23, 1985
San Clemente Island (SCL) Flasher Road Dunes	48	August 21, 1985
Ballona Wetlands (BA) (Los Angeles County)	48	June 9, 1985
El Segundo Dunes, LAX (ESG) (Los Angeles County)	36	April 15, 1985
Balboa Beach (NB) (Orange County)	48	April 14, 1985
Silverstrand State Beach (SVS) (San Diego County)	48	July 13, 1985
Punta Estero (PE) (Baja California Norte, Mexico)	48	October 15, 1985
Guerrero Negro (GN) (Baja California Sur, Mexico)	50	October 18, 1985

id groupings. Gertsch has recently reviewed morphological variation in this genus and all references to morphological differences are based on personal communication with him.

Phylogenetic analysis.—The problem of estimating phylogenetic trees from electrophoretic data has generated a wealth of divergent opinion, some of it couched in very strong language (reviewed by Felsenstein 1982; Buth 1984). While many methods for phylogenetic tree construction from electrophoretic data have been proposed (Felsenstein 1982; Swofford & Olsen 1990), none has been universally accepted (Quicke 1993; Avise 1994). Because of this lack of agreement, we used a variety of methods to analyze the electrophoretic data set for *Lutica*, using allele frequencies, alleles as discrete characters and genetic distances. These methods are based on the two main approaches that do not assume a constant rate of molecular evolution across all taxa being compared, maximum parsimony (Edwards & Cavalli-Sforza 1963) and maximum likelihood (Edwards & Cavalli-Sforza 1964; Felsenstein 1981). Comparison of the trees generated by the various methods indicates those portions of the phylogeny that are unaffected by the different assumptions of each method (i.e., different methods may yield similar branching patterns for some or all taxa) and which therefore may be assumed to represent more accurately actual

evolutionary relationships (Lanyon 1985; Avise 1994). Computer programs to carry out each of these methods are readily available. The particular programs/packages and specific computational procedures which were used are as follows:

Maximum parsimony: FREQPARS (version 1.0) (Swofford 1988) was used to conduct frequency parsimony analysis (Swofford & Berlocher 1987) of alleles at all loci, except those which were monomorphic across all populations (n) or $n - 1$ populations and therefore were phylogenetically uninformative. FREQPARS 1.0 has a very limited ability to search for the most parsimonious tree(s), so 19 runs of the data set were performed, with each OTU (operational taxonomic unit) in turn being placed first in the input file (following Rohlf & Wooten 1988). The shortest (i.e., most parsimonious) tree generated was retained.

HENNIG86 (version 1.5) (Farris 1988, 1989) was used for Wagner parsimony (Kluge & Farris 1969; Farris 1970) analysis of alleles as discrete characters, using presence/absence (1/0) coding for both complete (all alleles at frequencies > 0) and reduced (all alleles at frequencies $\geq$ 0.05) data sets (following Mickevich & Mitter 1981; C. Griswold pers. comm.), for all informative loci. The implicit enumeration (IE*) option of HENNIG86 was used to generate all most parsimonious trees for the complete and reduced

data sets, and then a strict consensus tree (Nelson 1979; Rohlf 1982) was computed for each set of most parsimonious trees.

BIOSYS-1 (version 1.7) (Swofford & Selander 1981, 1989) was used to perform distance Wagner analysis (Farris 1972; Swofford 1981) on a matrix of Rogers (1972) genetic distances for the *Lutica* populations; since Nei (1972, 1978) distances are non-metrical, which can result in negative branch lengths (Farris 1972; Nei 1987), they are not appropriate for use with distance Wagner analysis (Swofford 1981). Specifically, the DISWAG step call was invoked, with the multiple addition criterion (Swofford 1981) (maxtree = 30), Prager & Wilson's (1976) F goodness of fit criterion and outgroup rooting (Farris 1972) [with Guerrero Negro (GN) as outgroup] options. The shortest (i.e., most parsimonious) tree generated was retained.

Maximum likelihood: PHYLIP (versions 3.1 and 3.2) (Felsenstein 1988, 1989a, b) was used to generate maximum likelihood trees from the allele frequency data for the 19 *Lutica* populations using the CONTML program, with the G (global branch swapping), J (jumble addition, i.e., each OTU is added to the developing tree in random order) and O [outgroup rooting, with Guerrero Negro (GN) as outgroup] options invoked. Since CONTML does not perform exhaustive enumeration and evaluation of all possible tree topologies, the data set was run 19 times, with different random number seeds for the J option, following Felsenstein's (1981, 1989b) recommendation. Of the trees generated, the tree with the greatest likelihood was kept and the others were discarded.

Congruence. — Congruence among the phylogenies generated by the different methods was determined by the construction of consensus trees (reviewed by Rohlf 1982; Mickevich & Platnick 1989). In the present study, consensus trees were constructed for multiple trees generated by a single method (i.e., Wagner parsimony analysis of alleles as discrete characters with HENNIG86), as well as among the cladograms representing the best or consensus tree for each method. Because methods which generate multiple, equally likely trees might lead to misleading results with Adams (1972) consensus, strict consensus (Nelson 1979; Rohlf 1982) was used in such cases. On the other hand, in an effort to maximize taxonomic information, Adams consensus was used to determine congruence among the final (best or strict) trees produced by each method. To

quantitatively assess congruence among the phylogenies generated by the different methods, two consensus measures were calculated (following Rohlf 1982 and Rohlf et al. 1983): the normalized consensus fork (CF) index of Colless (1980) and the CI_I index of Rohlf (1982). Both congruence measures can range from 0.0 (totally dissimilar topologies) to 1.0 (identical topologies). The CONTREE program included with the PAUP (version 2.4.1) (Swofford 1985) computer package was used to generate consensus trees and calculate the consensus indices.

RESULTS

There were 43 alleles identified at the 15 genetic loci; two loci (APK-2 and G-3-PDH) were monomorphic across all populations and one locus (TPI-2) was autapomorphic (variable in only a single population) (Table 2). Tables of interpopulation genetic distances, mean genetic distances within and between *Lutica* species, and the data matrix of alleles coded as character states, which were used as the basis for some of the analyses reported herein, are available on request from the senior author.

Species identification. — The most striking feature of the allelic data (Table 2) is the genetic distinctness of the Guerrero Negro (GN) population: there are fixed differences at the FUM, HK and LDH loci; nearly fixed differences at the GPI (frequency of GPI-A = 0.990), IDH (frequency of IDH-C = 0.990) and PGM (frequency of PGM-A = 0.940) loci; and unique alleles at the AAT (AAT-A) and IDH (IDH-D) loci. In addition, the IDH-B allele, appearing at a frequency of 0.021 in only one other population [San Cruz Island (SCI)], is found at a frequency of 0.796 at Guerrero Negro. In light of the three fixed and three nearly fixed differences, the population of Guerrero Negro clearly represents a distinct species, our new species C. Spiders from this region are also a distinct group morphologically. Due to its genetic distinctness and the lack of certainty about which zodariid taxon would serve as an suitable outgroup for *Lutica*, Guerrero Negro was used as the outgroup in the phylogenetic analyses reported here.

In analyzing the data for the remaining populations for valid phylogenetic groups, the fixed difference at the NP locus is clearly indicative of common ancestry (and is not contradicted by data at other loci): populations 1–12 are fixed for NP-A and comprise our new species A. These are the mainland populations of Santa Barbara

and Ventura Counties, as well as the populations of the northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz) and three of the southern Channel Islands (San Nicolas, Santa Barbara, Santa Catalina). With the exception of Santa Barbara and Santa Catalina Islands, this is also a valid group morphologically.

As for the remaining populations (13–18), the electrophoretic data provide little basis for species decisions. The population of San Clemente Island (SCL), representing *clementea*, was not characterized by any fixed differences (Table 2) but did possess two unique alleles, though one was very rare: APK-1-A was found at a frequency of 0.132 and TPI-1-A was found at a frequency of 0.031. Among the mainland populations of southern California and northern Baja California, there were likewise no fixed differences that would conclusively indicate species status for any of these populations, though one locus indicated a close relationship between the populations of the Ballona Wetlands (BA) and El Segundo Dunes (ESG): at the PGM locus, the PGM-B allele was found at frequencies of 0.696 and 0.750 respectively and is found in only two other populations at frequencies of less than 0.05. Since the electrophoretic data are neutral with regard to the status of *clementea*, it will be accepted as a valid species. Likewise, while there are no allelic differences that would unite the mainland populations of southern California and northern Baja California as a group, morphological features define these populations as a distinct group (see also Thompson 1973). As such, they will be accepted as a valid species, our new species B.

Phylogenetic analysis.—We produced five estimates of the phylogeny of *Lutica* using methods which make no assumptions about evolutionary rates among taxa (i.e., frequency parsimony, distance Wagner, Wagner parsimony analysis of alleles as discrete characters and maximum likelihood). Trees generated by these methods have branch lengths which are proportional to the amount of evolutionary change which has occurred along each branch (Nei 1987; Swofford & Berlocher 1987). The trees generated by these methods for *Lutica* had branch lengths which were very unequal among the populations being compared. The distance Wagner tree (Fig. 2) is typical of the branch length variability which was present in all the trees; some populations (i.e., COP, MG, OX, LJB) have undergone considerable differentiation, while others (i.e., PE, NB) have changed much less. The unevenness of the

branch lengths indicate that allelic evolution in *Lutica* has certainly not been clocklike.

In order to simplify comparisons among the phylogenies produced by the four rate independent methods, they are presented as cladograms in which only the branching patterns are shown (following Richardson et al. 1986) (Figures 3–7). These cladograms are consistent in the definition of two monophyletic groups: A) the large group A (= new species A) appears in all the cladograms [in that based on Wagner parsimony analysis of alleles as discrete characters using the complete data set (alleles > 0.0) (Fig. 5), the population of San Clemente Island (SCL) is also included in this group]; B) the Los Angeles County populations of the Ballona Wetlands (BA) and the El Segundo Dunes (ESG) form a clade that appears in all the cladograms. Within group A, two clades are found in all the cladograms: one consisting of the population of Coal Oil Point Reserve (COP), Santa Barbara County, and the Ventura County populations of McGrath State Beach (MG), Oxnard Beach (OX) and La Jolla Beach (LJB) [reflecting their common possession of the PEP-C allele at frequencies ranging to fixation (Table 2)]; and the other comprised of the populations of San Nicolas Island [Red Eye Beach (SNE), Dutch Harbor (SND), Army Camp Beach (SNA)] and at least one of the northern Channel Islands, usually Santa Rosa (SRI) [reflecting their common possession, except for Santa Cruz Island (SCI), of the LDH-C allele in frequencies ranging to fixation (Table 2)]. These relationships are accurately represented in the Adams consensus tree for these cladograms (Fig. 8).

The populations of new species B (including the BA - ESG clade) and *clementea* are placed in various positions among the five cladograms, with no consistent pattern of relationship, not surprising given the inconclusiveness of the electrophoretic data for these populations. San Clemente Island (*clementea*) is placed as the sister group to new species A in two cladograms (Figs. 3, 7); as sister group to new species A along with the populations of Balboa Beach (NB) and Punta Estero (PE) in one (Fig. 4); and as sister group to new species A along the with populations of the Ballona Wetlands (BA) - El Segundo Dunes (ESG) clade, Balboa Beach (NB) and Punta Estero (PE) in another (Fig. 6). As mentioned earlier, the remaining cladogram (Fig. 5) places San Clemente as part of new species A. The Adams consensus tree (Fig. 8) reconciles these differences by placing SCL, NB and PE as sister group

Table 2.—Allele frequencies in 19 populations of *Lutica* in California and Baja California. Species abbreviations are: CLE, *clementea*; NSP C, new species C. Population abbreviations follow Table 1.

Locus / Allele	New species A												CLE		New Species B				NSp C
Allele	COP	MG	OX	LJB	SMI	SRI	SCI	SBI	SNE	SNA	SND	CAT	SCL	BA	ESG	NB	SVS	PE	GN
Mean n	45	45	33	44	44	44	44	44	22	21	19	45	45	45	33	44	45	45	46
AAT																			
A																			0.010
B							0.021												0.796
C	1.000	1.000	1.000	1.000	1.000	0.979	0.979	1.000	1.000	1.000	1.000	0.948	1.000	1.000	1.000	1.000	1.000	1.000	0.194
D						0.021						0.052							
APK-1																			
A													0.132						
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.971	1.000	1.000	1.000	1.000	0.868	0.971	1.000	0.969	1.000	1.000	1.000
C								0.029						0.029		0.031			
APK-2																			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
FUM																			
A						0.011		0.152											
B								0.152							0.044				
C	1.000	1.000	1.000	1.000	1.000	0.924	1.000	0.696	1.000	1.000	1.000	1.000	1.000	1.000	0.941	1.000	1.000	1.000	1.000
D						0.065									0.015				
G-3-PDH																			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI																			
A	0.417	0.021						0.010	0.042			0.021		0.010			0.083	0.021	0.990
B	0.583	0.979	1.000	1.000	0.958	0.979	1.000	0.990	0.958	1.000	1.000	0.969	0.990	0.990	1.000	1.000	0.917	0.979	0.010
C					0.042	0.021						0.010	0.010						
HK																			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
B																			1.000
IDH																			
A	0.010																		
B	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.979	1.000	1.000	0.875	1.000	1.000	1.000	1.000	0.865	1.000	
C									0.021			0.125					0.135		0.990
D																			0.010

Table 2.—Continued.

Locus / Allele	COP	MG	OX	LJB	SMI	SRI	SCI	SBI	SNE	SNA	SND	CAT	SCL	BA	ESG	NB	SVS	PE	GN
	New species A												CLE	New Species B					NSp C
Mean n	45	45	33	44	44	44	44	44	22	21	19	45	45	45	33	44	45	45	46
LDH																			
A																			
B	1.000	1.000	1.000	1.000	0.587	0.011	0.967	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.969	1.000
C					0.413	0.989	0.033											0.031	
MDH																			
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.958	1.000	1.000	0.500	1.000	0.990	0.972	1.000	1.000	1.000	1.000
B									0.042					0.010	0.014				
C												0.500			0.014				
NP																			
A													0.021						
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.979	1.000	1.000	1.000	1.000	1.000	1.000
PEP																			
A	0.177	0.362	0.277																0.490
B	0.760	0.170	0.168		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.290
C	0.063	0.468	0.555	1.000															0.220
PGM																			
A														0.011					
B									0.042		0.025			0.696	0.750				
C																	0.219		
D	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.958	1.000	0.975	1.000	1.000	0.293	0.250	1.000	0.781	1.000	1.000
E																			
TPI-1																			
A													0.031						
B	1.000	0.969	0.500	0.187	1.000	0.969	1.000	1.000	1.000	1.000	1.000	1.000	0.969	1.000	1.000	1.000	1.000	1.000	1.000
C		0.031	0.500	0.813		0.031													
TPI-2																			
A					0.098														
B	1.000	1.000	1.000	1.000	0.902	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Figure 2.—Phylogenetic tree generated using distance Wagner method (Farris 1972; Swofford 1981) with multiple addition criterion (Swofford 1981) and outgroup rooting (Farris 1972), with Guerrero Negro (GN) as outgroup. The distance measure used is Rogers (1972). Total length of tree = 0.984 and Prager & Wilson's (1976) $F = 4.985$.

to new species A. Finally, in four of the five cladograms (Figs. 3, 5–7), the population of Silverstrand State Beach (SVS) is placed as the sister group to all other ingroup populations, while in the one exception (Fig. 4), the BA - ESG clade is placed in this position. The consensus tree resolves this difference by placing both SVS and the BA - ESG clade as sister group to all other populations (Fig. 8). This last feature of Fig. 8 illustrates one of the problems with Adams consensus trees: in none of the original cladograms is a clade comprised of SVS and BA - ESG placed as the sister group to all other ingroup populations. Given the differences in topology among these cladograms, it is not surprising that consensus indices for the Adams consensus tree are not high: Colless' (1980) CF = 0.471 and Rohlf's (1982) $CI_1 = 0.400$.

To focus specifically on the phylogenetic relationships of the species themselves, the population data for new species A and B were combined into single species samples and the analyses reported above were repeated for the four OTUs (new species A, B, C, *clementea*), with the sole exception that Wagner parsimony of alleles as discrete characters was not performed for the

reduced data set (alleles ≥ 0.05), due to the exclusion of practically all alleles under such a restriction. The cladograms produced by each method are shown in Fig. 9, A–D and the Adams consensus tree is shown in Fig. 9E. For three OTUs, there are three possible relationships [A(BC), C(AB), B(AC)] and all three are seen for the ingroup taxa among the cladograms in Fig. 9, A–D, although those produced by frequency parsimony (A) and maximum likelihood (D) are identical and place new species B and *clementea* as sister groups, as might be expected given their minimal genetic distance [Nei (1978) unbiased genetic distance: 0.017 (Ramirez 1990)]. Since the topologies of these cladograms covered all the possibilities for a three taxon statement, the Adams consensus tree presents the relationships among the three ingroup species as a unresolved trichotomy, although the consensus indices for this tree were fairly good [Colless' (1980) CF = 0.500 and Rohlf's (1982) $CI_1 = 0.667$], reflecting the perfect agreement between two cladograms. Thus, while two of the cladograms agreed in the placement of new species B and *clementea* as sister groups, these results were contradicted by the topologies of the other two cladograms, so
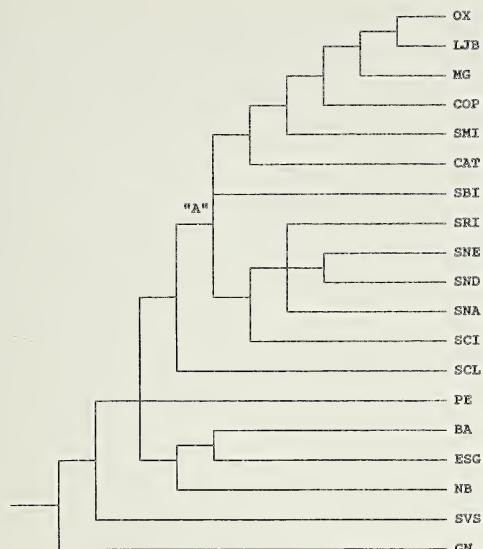
Figure 3.—Cladogram for *Lutica* based on the shortest tree generated using the frequency parsimony method (Swofford & Berlocher 1987) and outgroup rooting (Farris 1972), with Guerrero Negro (GN) as outgroup. The frequency parsimony method minimizes tree length in the Manhattan metric (Sneath & Sokal 1973); total length of shortest tree = 29.509. Alphabetic designation "A" denotes new species A.

Figure 4.—Cladogram for *Lutica* based on the shortest tree generated using the distance Wagner method (Farris 1972; Swofford 1981), which is shown in Fig. 2. Alphabetic designation "A" denotes new species A.

the electrophoretic data were not able to conclusively determine phylogenetic relationships among the ingroup species.

DISCUSSION

Electrophoresis and morphology.—The genus *Lutica* occupies a long geographic range (approximately 1857 km) yet is relatively invariant morphologically. Gertsch (pers. comm.) uses features of the male palpi to discriminate species and only in *clementea* and the populations of central and southern Baja California are the differences in these structures clearly distinct. An analysis of variation among *Lutica* specimens involving 23–29 morphological characters (Thompson 1973) did not find statistically significant differences (M. Thompson pers. comm.).

The genus *Lutica* is also relatively invariant genetically: Ramirez (1990) found low levels of genetic variability among *Lutica* populations, as well as a general trend toward within population homozygosity. As a presumably old genus (Ramirez 1990), the existence of low genetic variability was unexpected and an analysis of the genetic structure of each species suggests that inbreeding, a spatial Wahlund effect due to local

probabilities of random mating and environmental homogeneity associated with a subterranean existence in coastal dune ecosystems may be the most likely causes of low variability in *Lutica* (Ramirez 1990).

The electrophoretic data define an outgroup [Guerrero Negro (GN), new species C] and two nested ingroups: first, populations 1–18, and nested within that, populations 1–12 (new species A). Morphological data indicate the specific distinctness of the population of San Clemente Island (*clementea*) (Gertsch 1961, pers. comm.), whereas the electrophoretic data were neutral. The electrophoretic data were likewise inconclusive with regard to the status of the mainland populations of southern California and northern Baja California but since they are morphologically a valid group, they are assigned to new species B. Future electrophoretic studies involving more loci (only 12 of the 15 loci were phylogenetically informative) may eventually result in the discovery of diagnostic loci for these mainland populations (new species B), as well as for *clementea*.

The morphological systematics of the genus *Lutica* has been in a state of flux for many years (M. Thompson pers. comm.; W. Gertsch pers. comm.) and electrophoretic variation (particularly fixed allelic differences) is probably a more
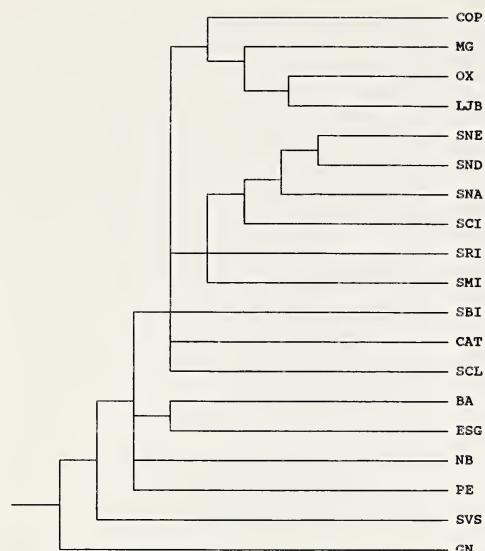
Figure 5.—Cladogram for *Lutica* based on strict consensus tree (Nelson 1979; Rohlf 1982) of 10 trees of 43 steps each with consistency indices of 0.442 generated using Wagner parsimony (Kluge & Farris 1969; Farris 1970), with alleles treated as characters with frequency greater than 0 = present. Consistency index = 0.410.

Figure 7.—Cladogram for *Lutica* based on the tree of highest likelihood generated by the restricted maximum likelihood method (Felsenstein 1981) and outgroup rooting (Farris 1972), with Guerrero Negro (GN) as outgroup. Ln Likelihood = 879.074. Alphabetic designation "A" denotes new species A.
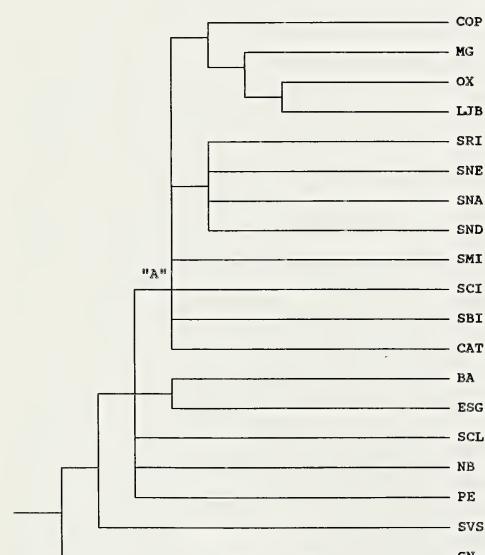
Figure 6.—Cladogram for *Lutica* based on strict consensus tree (Nelson 1979; Rohlf 1982) of eight trees of 21 steps each with consistency indices of 0.610 generated using Wagner parsimony (Kluge & Farris 1969; Farris 1970), with alleles treated as characters with frequency greater than or equal to 0.05 = present. Consistency index = 0.590. Alphabetic designation "A" denotes new species A.

reliable indicator of taxonomic relationships than morphological features for this genus. An obvious disagreement between our species assignments and those of Gertsch (1961) concerns the status of the populations of San Nicolas and Santa Rosa Islands and Oxnard, Ventura County: each is considered a distinct species (*nicolasia*, *maculata* and *abalonea*, respectively), while we place them all in new species A. Due to the fixed difference at the NP locus, the assignment of these populations to new species A is unambiguous on genetic grounds. Gertsch (pers. comm.) began a revision of *Lutica* prior to his deteriorating health and so a detailed comparison of the population groupings indicated by morphological and electrophoretic characters will have to await its completion and publication.

Phylogeny and speciation in *Lutica*.—The fact that the genetic distance between new species B and *clementea* (0.017) is several orders of magnitude less than the other inter-specific estimates [0.138–0.796, all Nei (1978) unbiased distances (Ramirez 1990)] would suggest that these taxa were originally a single species that only recently diverged. If this is the case, one would predict that these species should be placed as sister groups in any phylogeny, as a clade that is the sister group to new species A. However, while this was
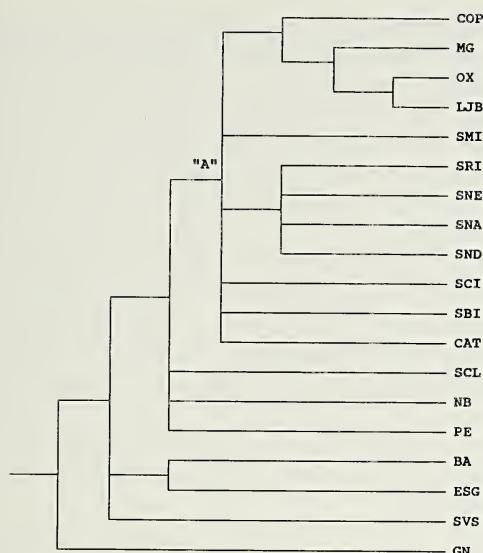
Figure 8.—Adams (1972) consensus tree based on cladograms of Figs. 3–7. Consensus indices for this tree are: Colless' (1980) CF = 0.471 and Rohlf's (1982) CI$_1$ = 0.400. Alphabetic designation "A" denotes new species A.

the case in two of the species cladograms (Fig. 9A, D), these relationships were contradicted by the topologies of the other two cladograms (Fig. 9B, C).

It should be noted that the two cladograms which depict new species B and *clementea* as sister groups (Fig. 9A, D) are the products of phylogenetic methods (frequency parsimony and maximum likelihood) which use allele frequency data directly. Methods which use allele frequencies may be superior because they avoid the loss of phylogenetic information and the procedural/theoretical complexities associated with the reduction of such data to distances or characters (Berlocher 1984; Swofford & Berlocher 1987). On the other hand, allele frequencies are subject to the effects of random drift and/or selection and can vary over time, and so may not provide reliable information for analysis (Crother 1990). Given the continuing controversy about allele frequencies and the potential superiority of phylogenetic methods which make direct use of them (e.g., Shaffer et al. 1991; Jones et al. 1993), a firm conclusion concerning the relationship of new species B and *clementea* within *Lutica* will have to await a future phylogenetic analysis.

Biogeography of *Lutica* in southern California and Baja California.—The phylogenetic relationships among the populations consistently
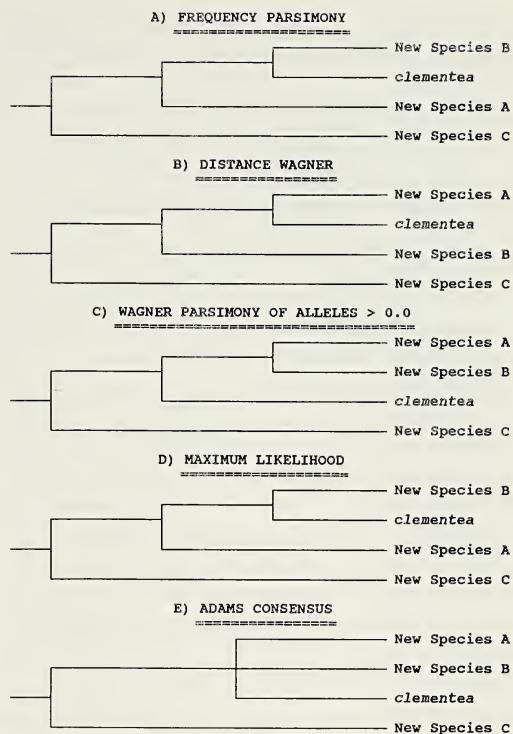
Figure 9.—Cladograms for *Lutica* species. (A) Cladogram based on the shortest tree generated using the frequency parsimony method (Swofford & Berlocher 1987) and outgroup rooting (Farris 1972), with new species C (Guerrero Negro) as outgroup. The frequency parsimony method minimizes tree length in the Manhattan metric (Sneath & Sokal 1973); total length of shortest tree = 18.160. (B) Cladogram based on the shortest tree generated using the distance Wagner method (Farris 1972; Swofford 1981), with multiple addition criterion (Swofford 1981) and outgroup rooting (Farris 1972), with new species C (Guerrero Negro) as outgroup. The distance measure used was Rogers (1972). Total length of shortest tree = 0.616 and Prager & Wilson's (1976) F = 1.857. (C) Cladogram based on the shortest tree generated using Wagner parsimony (Kluge & Farris 1969; Farris 1970), with alleles treated as characters with frequency greater than 0 = present. Total length of shortest tree = 16 steps and consistency index = 0.680. (D) Cladogram based on the tree of highest likelihood generated by the restricted maximum likelihood method (Felsenstein 1981) and outgroup rooting (Farris 1972), with new species C (Guerrero Negro) as outgroup. Ln Likelihood = 53.788. (E) Adams (1972) consensus tree based on cladograms presented in A–D. Consensus indices for this cladogram are: Colless' (1980) CF = 0.500 and Rohlf's (1982) CI$_1$ = 0.667.

supported by the electrophoretic cladograms and depicted in the Adams consensus tree (Fig. 8) reflect the evolutionary relationships of these fossorial spiders and suggest probable scenarios for the historical colonization of some of the Channel Islands. In most instances, the electrophoretic data correspond well with the known geological history of the islands and adjacent mainland. During the late Pleistocene, eustatically lowered sea levels united the four northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa) into a single land mass, Santarosae (Orr 1968). Santarosae began its final breakup only about 16,000 years ago (Vedder & Howell 1980; Johnson 1983). The former physical connection of San Miguel, Santa Rosa and Santa Cruz Islands appears to be reflected in the close genetic relationship of the *Lutica* populations of these islands: all three island populations are members of new species A and in four of the five cladograms (Figs. 3–5, 7), at least two of these three islands are placed in the same clade within new species A. In contrast, the southern Channel Islands (San Nicolas, Santa Barbara, Santa Catalina, San Clemente) were never physically connected (Vedder & Howell 1980; Johnson 1983). Since two of these islands (San Nicolas and Santa Barbara) were submerged during the middle Pleistocene (Johnson 1983), they derived their biota from other sources since that time. The fact that the *Lutica* populations of the two southern islands which were not submerged, Santa Catalina and San Clemente, are considered to be very different on both electrophoretic and morphological grounds is indicative of the absence of significant gene flow that would have been provided by an inter-island connection and may reflect the fact that these islands were originally far apart, prior to San Clemente's arrival at its present location due to terrane transport (Crouch 1979; Hornafius et al. 1986).

The mainland populations of new species A and B are only about 57 km apart at their southern and northern boundaries respectively [between La Jolla Beach (LJB), Ventura County and the Ballona Wetlands (BA), Los Angeles County] yet spiders from these regions are members of different taxa. This disjunction may simply reflect the fact that there are no relatively continuous dune systems in the intervening coastal area between Ventura County and Los Angeles (Cooper 1967; Powell 1981) which might act as a corridor for gene flow between these species. On the other hand, this disjunction may be associ-

ated with geologic changes that occurred in this region beginning in the Pliocene. During this time the Los Angeles basin was flooded (Murphy 1983a), which, coupled with the northward extension of the Sea of Cortez, caused complete isolation or severe restriction of the movements of organisms to and from Baja California at its northern end (Durham & Allison 1960), a situation which lasted till the Pleistocene (Murphy 1983a). This so called San Gorgonio Barrier has been implicated as a historic biogeographic obstacle for the movement of certain xeric-adapted reptiles (Murphy 1983b) and may be at least partly the cause of the disjunction between the mainland populations of *Lutica* from its northern (new species A) and central (new species B) mainland regions.

The Vizcaino Peninsula has alternately been united with and separated from Baja California by sea level changes since the Eocene (Durham & Allison 1960; Murphy 1983a). Since an arid desert lies between this region and the northern portion of Baja (Crosswhite & Crosswhite 1982), it is probable that the divergence between the *Lutica* populations of the Vizcaino Peninsula and those of northern Baja California is an ancient one, as has been shown for the vegetation of these regions (Axelrod 1979, 1980). The considerable genetic and morphological differences between the population of Guerrero Negro (new species C) and populations to the north is consistent with the geologic history outlined above and indicates a long absence of gene flow between spiders of these two regions.

Patterns of colonization.—Some of the genetic relationships are indicative of certain likely colonization events involving the Channel Islands. These will be reviewed for each island or group of islands in the sections which follow.

Northern Channel Islands, Santa Barbara and San Nicolas Islands: The populations of San Nicolas Island were consistently most closely grouped with one of the northern Channel Islands (usually Santa Rosa), indicating probable colonization of this formerly submerged southern Channel Island from the islands 80 km to the north. Santa Barbara Island was also submerged in the Pleistocene and is also a member of new species A. Since there is no particular population(s) with which it is consistently grouped, all that can be deduced is that colonists of Santa Barbara were derived from one of the new species A populations, most of which are located to the north. In the case of both San

Nicolas and Santa Barbara, rafting colonists from the north would have been aided by south flowing ocean currents and prevailing northwest winds that have been implicated in the dispersal of other organisms in this region (examples in Power 1980; Cowen 1985), as well as the south flowing longshore current (Ledig & Conkle 1983). However, the ocean current patterns in this region are not invariant and the southward flowing California Current is known to reverse its direction during El Niño events (Cowen 1985), perhaps making it possible for propagules to drift northward from Santa Catalina Island to Santa Barbara Island.

The fact that the *Lutica* populations of the northern Channel Islands and adjacent mainland of Santa Barbara and Ventura Counties are members of the same species is typical of the close relationships that have been reported for island and mainland populations of other organisms in this region (e. g., sand crickets, Rentz & Weissman 1973; Weissman & Rentz 1976; deer mice, Ashley & Wills 1987). Indeed, 89% of the orthopteran fauna of the northern Channel Islands also occurs in the Santa Monica Mountains (Rentz & Weissman 1981). While the general interpretation of such distributions and relationships has been that colonists from the adjacent mainland founded the island populations (Rentz & Weissman 1981; Ashley & Wills 1987), the geologic relationships among the islands and mainland were considerably different in the past, rendering considerations of dispersal among what may be recent subdivisions possibly suspect. For example, the northern Channel Islands were situated as much as 8° to the south of their present locations during the middle Miocene, prior to northward transport on a terrane (Kamerling & Luyendyk 1985). The southern origin for these islands may mean that the actual colonists of these islands came from mainland populations of southern California or Baja California. On the other hand, the populations of these islands and the adjacent mainland were perhaps established at more or less the same time by colonists from San Clemente Island or mainland populations of new species B. While these and other colonization scenarios may be plausible, the electrophoretic data do not allow one to determine directions of colonization between the island and mainland populations of new species A, nor do they establish the actual sister group of this species, rendering consideration of mainland-island

colonization scenarios involving populations of this species unwarranted at this time.

Santa Catalina Island: Since Santa Catalina Island (along with Santa Rosa and Santa Cruz Islands) may have been continuously above water since the Oligocene (Vedder & Howell 1980; Haq et al. 1987), has remained relatively stationary during this period (Luyendyk et al. 1985) and is close to the southern California mainland, one would expect that its closest biotic relationship should be with populations from the adjacent Los Angeles–San Diego coastal strip. However, we have shown that the *Lutica* population of Santa Catalina is most closely related to new species A populations rather than populations on the southern California mainland. The most parsimonious explanation for such a relationship is that spiders from the adjacent mainland never colonized Santa Catalina and so new species A spiders were the first and only colonists. On the other hand, such a pattern of relationships may be due to the extinction of an original insular form derived from the mainland prior to colonization by new species A spiders or because new species A spiders proved to be superior in competition with the native insular form. Separate colonizations of Santa Catalina Island from the northern Channel Islands and southern California mainland have been proposed for Channel Island deer mice, *Peromyscus maniculatus*, due to mitochondrial DNA restriction fragment polymorphisms found among Santa Catalina Island mice (Ashley & Wills 1987). Extinction has also been suggested to explain the distribution of the island night lizard, *Klauberina*, which is found on San Clemente, San Nicolas and Santa Barbara Islands but not on Santa Catalina Island (Crother et al. 1986; Bezy & Sites 1987).

San Clemente Island: A biogeographic relationship between San Clemente Island and Baja California has been proposed by Crother et al. (1986), based on a cladistic study of morphology and karyology within the lizard family Xantusiidae and a vicariance model based on terrane movement linking San Clemente and central Baja California. Based on geophysical evidence (Crouch 1979; Hornafius et al. 1986), it is clear that San Clemente Island was in close proximity to central Baja California up to about 18 million years ago, when the terrane on which it is situated started moving north along the San Clemente Island Fault, eventually reaching its present position about 5–8 million years ago. Crother et al. (1986) hypothesize that relatively sedentary taxa

(like xantusiid lizards) which occupied San Clemente Island and the adjacent mainland of Baja California prior to the time of northward movement (and whose descendants continue to occupy these areas today) should be closely related.

Since *Lutica* is clearly sedentary and has distinct species which occupy San Clemente Island (*clementea*) and central Baja California (new species C), we hoped to be able to test Crother et al.'s (1986) vicariance hypothesis using the electrophoretic data reported herein. However, given the need to use Guerrero Negro (new species C) as an outgroup in our phylogenetic analyses, in the absence of an appropriate zodariid taxon, it was not possible to determine whether *clementea* is indeed most closely allied with new species C of central Baja California. As such, a final decision concerning *Lutica*'s involvement in the biogeographic hypothesis of Crother et. al. (1986) will have to await a future phylogenetic analysis using an actual outgroup taxon.

SUMMARY

The geological history of the California Channel Islands and mainland of southern California and Baja California involves extensive sea level changes and the movement of terranes. These geomorphic changes may have influenced the evolution of taxa in this region, particularly if they are sedentary and biologically old.

Analysis of the results of an electrophoretic survey of populations of the spider genus *Lutica* from much of its range revealed fixed allelic differences that clearly define two species: new species A [Santa Barbara and Ventura Counties, northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz), southern Channel Islands (San Nicolas, Santa Barbara, Santa Catalina)] and new species C [Guerrero Negro, central Baja California]. While diagnostic loci were not found for the population of San Clemente Island (*clementea*) or the mainland populations of southern California and northern Baja California, they are morphologically recognizable units according to Gertsch, so *clementea* was accepted as valid, while the mainland populations were assigned to new species B.

Phylogenetic analysis of the electrophoretic data using a variety of methods revealed that evolutionary rates among the 19 populations sampled have been very unequal. The phylogenetic relationships among populations consistently supported by the electrophoretic cladograms generally correspond with the geological

history of the Channel Islands and adjacent mainland and suggest certain likely colonization events involving some of the islands.

A future electrophoretic study of *Lutica* involving more loci and a zodariid taxon as an outgroup (chosen in light of Jocqué 1991) is needed to A) genetically validate the species status of the mainland populations of southern California and northern Baja California, as well as of *clementea*, and B) to resolve the phylogenetic relationships among the four species (new species A, B, C, *clementea*). Further systematic studies of other monophyletic taxa (particularly those which are biologically old and poor dispersers) occupying the California Channel Islands and mainland of southern California and Baja California are needed to better understand the geologic and biogeographic evolution of this region. Given the lack of even basic knowledge concerning many taxonomic groups in this area, particularly among the invertebrates, this will be a fruitful area for the conduct of systematic and biogeographic studies.

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REDESCRIPTION OF *STENOSTYGNUS PUSIO* SIMON AND SYNONYMY OF CARIBBIANTINAE WITH STENOSTYGNINAE (OPILIONES: LANIATORES, BIANTIDAE)

Ricardo Pinto-da-Rocha: Museu de Zoologia, Universidade de São Paulo, Caixa Postal 7172, São Paulo, SP, Brazil, 01064-970

ABSTRACT.   Based on the lack of the tarsal process and genitalic features, *Stenostygnus pusio* Simon 1879 is transferred from the Stygnidae to the Biantidae. This is the first record of the family Biantidae from Brazil, Colombia and Ecuador. The subfamily Caribbiantinae is synonymized with Stenostygninae. Genera and species other than *Stenostygnus pusio*, formerly placed in the Stenostygninae are transferred to Heterostygninae (Stygnidae). The convergences between Stygnidae and Biantidae are presented and discussed.

Stenostygnus pusio Simon 1879 was described based on a single female from Tefé (Amazonas, Brazil) and included in the then created new subfamily of Gonyleptidae, Stygninae. Roewer (1913) established the subfamily Stenostygninae for *Stenostygnus* Simon and *Stenostygnellus* Roewer. Sørensen (1932) erected the family Stygnidae for the Gonyleptidae subfamilies without a common eye mound (Heterostygninae, Phareinae, Stenostygninae and Stygninae). Up to now, *S. pusio* was known only by the holotype. Caporiacco (1951) described *Stenostygnus magnus* from Venezuela.

The study of *Stenostygnus pusio*, especially of the male genitalia, showed me that this species belongs to the Biantidae. The external characters included it in the Caribbiantinae, which is a junior synonym of Stenostygninae.

The specimens studied are deposited in: Museu de Zoologia da Universidade de São Paulo, São Paulo (MZSP); Museu de Ciências Naturais, Porto Alegre (MCN); Museum of Comparative Zoology, Cambridge (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); and the National Museum of Natural History, Washington (USNM). All measurements are in millimeters.

Biantidae Thorell

Biantidae Thorell 1889: 670; Sørensen, 1932: 224; Martens, 1978: 358; Shear, 1982: 107.

Diagnosis.—Cephalothorax almost as wide as abdomen. Eye mounds separate. Chelicera segment I smooth, condyle-like. Tarsi III-IV with or without scopulae; without tarsal process. Penis with titillators and conductors; stylus long and thin.

Subfamilies included.—Biantinae, Dibuninae, Stenostygninae and Zairebiantinae. However, the opiliologists are not unanimous as regards composition of the subfamilies of the Biantidae. Roewer (1923) considered all subfamilies as members of Phalangodidae, Sørensen (1932) considered Dibuninae as a family, but Martens (1978) and Shear (1982) did not consider Caribbiantinae (now Stenostygninae) as a Biantidae and finally, Martens (1978) considered Dibuninae as a Phalangodidae member.

Stenostygninae Roewer

Stenostygninae Roewer 1913: 163; 1923: 459; Mello-Leitão 1932: 418.
Caribbiantinae Šilhavý 1973: 133; Avram 1977: 123.SYN. N.

Diagnosis.—Eye mounds near groove I. Four areas on dorsal scute, area I with or without median groove. Male chelicera swollen or not swollen. Pedipalps long and thin; dorsally unarmed; coxa conical; patella with or without mesoapical seta. Tarsi III-IV with scopulae of spatulate hairs; claws smooth and opposite; distitarsus I with three and II with four segments. Metatarsus III spindled. Penis without membranous region in the ventral plate.

Stenostygnus Simon

Stenostygnus Simon: 1879: 219, 224; Roewer 1913: 163; 1923: 460; Mello-Leitão 1932: 418 (type species: *Stenostygnus pusio* Simon 1879, by monotypy).

Diagnosis.—Differs from the other Stenostygninae genera by the lack of spines or prominent
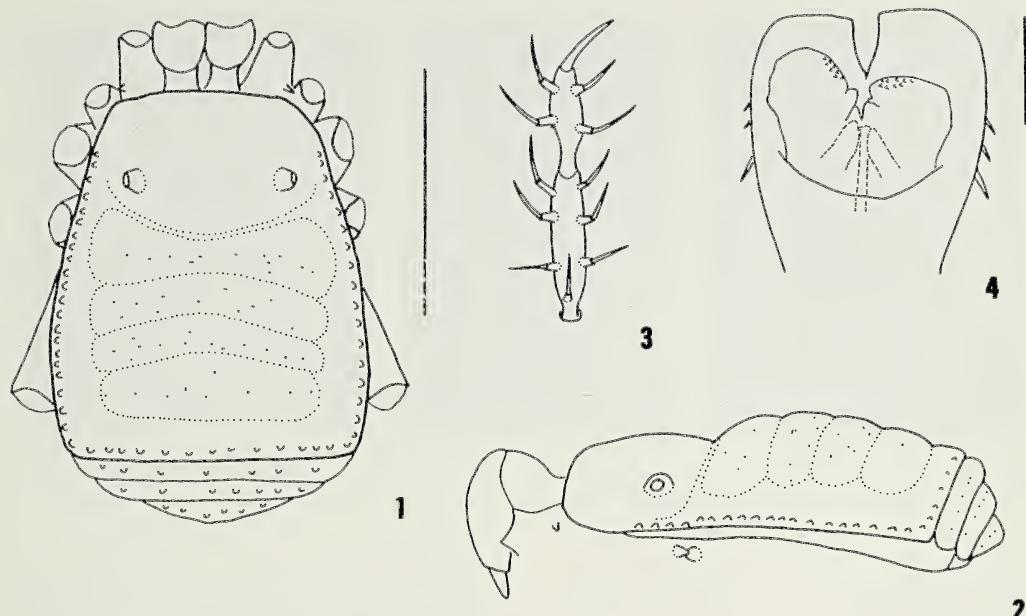
Figures 1–4.—*Stenostygnus pusio* Simon, female holotype. 1, Habitus, dorsal view; 2, Lateral view; 3, Ventral view of left pedipalp, tibia and tarsus; 4, Dorsal view of distal part of penis. Scale bar: Figs. 1–3 = 1.0 mm; Fig. 4 = 0.5 mm.

tubercles on dorsal scute; male chelicera not swollen; pedipalpal patella without apical setae; male tarsus I with 8 segments, instead of 5–7.

Stenostygnus pusio Simon
Figs. 1–7

Stenostygnus pusio Simon 1879: 224; Roewer 1913: 163, fig. 71 (redescription); 1923: 460, fig. 578 (redescription); Mello-Leitão: 1923: 133 (citation); 1932: 419 (redescription). (holotype female "Teffé, coll. Simon, Paris, n° 4007, type" MNHN, examined).

Male description.—(USNM). *Measurements:* Dorsal scute 1.54 long, 1.22 wide; cephalothorax 0.66 long, 1.10 wide. Chelicera: segment II 0.66 long, III 0.22 long. *Dorsal scute:* (Figs. 1, 2). Cephalothorax and eyes mounds smooth. Anterior margin slightly raised laterally. Areas I–IV undivided and with minute tubercles. Lateral margin with one row of large tubercles from coxa III to posterior margin. Posterior margin with one row of large tubercles, median row of tubercles smaller. Free tergites I–III with one row of small tubercles. Anal opercle tuberculate. *Venter:* Coxae I–III with minute tubercles, lacking apically; coxa IV smooth. Stigmatic area smooth, long; stigmae concealed; free sternites with one transversal row of minute tubercles. Anal opercle tuberculate. *Chelicera:* Segment I smooth, II not swollen; chelicera fingers with teeth. *Pedipalps:* Coxa with two ventral tubercles; trochanter smooth; femur straight, without ventrobasal tubercle; patella swollen at apical third; tibia (Fig. 3) with one ventrobasal seta and three longer setae on each side. Tarsus (Fig. 3) with two long setae on each side. *Legs:* Long, straight and thin. Patela IV with three prolateral tubercles and one dorsoapical. Tarsal claws smooth, double and lying perpendicular to the axis of the leg. Scopulae dense on last segment, with spatulate hairs. Tarsal segmentation: 8(3), 12(4), ?, 6. The specimens examined lacked the third pair of legs. *Penis:* (Figs. 5–7). Ventral plate with an apical cleft "U" shaped; with five retrolateral pairs of setae and two subapical ventral pairs of bifid setae. With titillators; stylus and conductors concealed by the titillators. *Coloration:* Brownish, pedipalpus yellowish.

Female supplemental description (holotype).— *Measurements:* Dorsal scute 1.40 long, 1.92 wide; cephalothorax 0.52 long, 1.16 wide. Chelicera: segment II 0.52 long, III 0.26 long. (Measurements of appendages in Table I.)

Female similar to the male. Lateral margin of dorsal scute with a row of large tubercles from coxa II to posterior margin. Patella IV without tubercles. Tarsal segmentation: 6(3), 9(3), 6, 6.

Figures 5–7.—*Stenostygnus pusio* Simon. Scanning electron micrographs of distal part of penis (USNM). 5, Dorsal view; 6, Lateral view; 7, Ventral view. Scale bar = 0.2 mm.

Type locality.—Tefé, Amazonas, Brazil (03°22′S - 64°42′W).

Distribution.—Recorded from Amazon basin (Colombia, Ecuador and Brazil). All records were made from localities near the tributaries of Amazon/Solimões river. Roewer (1913, 1923) recorded the "type" as being from Cayenne (French Guiana) and a second specimen, not belonging to the type series, from Tefé (Brazil). I examined the holotype and it was labeled "Teffé" as in Simon's description. There are no other specimens of *S. pusio* in the MNHN, and I think that Roewer was mistaken.

Material examined.—BRAZIL. *Amazonas:* Tefé, ♀ holotype (MNHN); Solimões River, 30 April 1966, 3♂ (USNM); Alto Solimões, 20 December 1979, A. Lise *leg*, 1♀ (MCN). **COLOMBIA.** *Amazonas:* Amacayacu (National Parq 48 km NW from Leticia, 03°48′S, 70°16′W), 90–100 m, 3 October 1985, 1♀ (MCZ). **ECUADOR.** *Napo:* Pompeya (Napo river), May 1965, Peña *leg*, 1♀ (MCZ).

DISCUSSION

Simon (1879) described *Stenostygnus pusio* within the Gonyleptidae, subfamily Stygninae. Simon's subfamily, characterized by the lack of a common eye mound, was divided by Roewer (1913) into four separate subfamilies: Heterostygninae, Phareinae, Stenostygninae and Stygninae. Stenostygninae was established for two monotypic genera, *Stenostygnellus* (with one species, *S. flavolimbatus* Roewer 1913) and *Stenostygnus*. Later, the following genera and species were described in the Stenostygninae: *Bunistyg-*

nellus beebei Goodnight & Goodnight 1949; *B. macrochelis* Roewer 1916; *B. ornatus* Roewer 1943; *Dichobunistygnus ephippiatus* Roewer 1915; *Hoplostygnus albicinctus* Roewer 1915; *Stenostygnellus praetiosus* Caporiacco 1951; *Xanthostygnus fractus* Mello-Leitão 1949 and another species of *Stenostygnus* (*S. magnus* Caporiacco 1951).

During the review of the family Stygnidae (Pinto-da-Rocha unpubl. data), I examined the holotype and some other specimens of *S. pusio*. I didn't observe a tarsal process on legs III–IV and from the examination of the genitalic features, I concluded that there is no evidence to place *Stenostygnus* in the Stygnidae. Simon (1879) stated that the holotype had a well developed pseudonychium (= tarsal process) and pectinate claws, but I observed only a long hair and smooth claws. The presence of a tarsal process is synapomorphic for Cranaidae + Gonyleptidae + Cosmetidae + Stygnidae (Kury 1992). The tarsal process is historically an important feature to distinguish the families of Gonyleptoidea without the common eye mound: Podoctidae/Biantidae/Stygnommatidae (tarsal process absent) from Stygnidae (present). However, some species of Stygnidae have secondaryly lost the tarsal process (e. g., *Auranus*, *Pickeliana*, unpubl. data). The genitalic features (presence of titillators) confirm the position of *S. pusio* in Biantidae.

The Biantidae are currently divided in four subfamilies: Biantinae, Stenostygninae (= Caribbiantinae), Dibuninae and Zairebiantinae. Biantinae have scopulae, four areas on dorsal scute and parallel claws; Stenostygninae have four

Table 1.—Appendage measurements of the female holotype of *Stenostygnus pusio* Simon. Tr = trochanter, Fe = femur, Pt = patella, Ti = tibia, Mt = metatarsus, Ta = tarsus. Measurements are in mm.

	Tr	Fe	Pt	Ti	Mt	Ta	Total
Leg I	0.16	1.40	0.32	1.00	1.48	0.92	5.28
II	0.26	3.36	0.44	2.96	4.60	1.76	13.38
III	0.20	2.28	0.36	1.20	2.50	0.78	7.32
IV	0.26	3.20	0.48	1.62	3.96	0.82	10.34
Pedipalp	0.22	1.10	0.64	0.56	—	0.40	2.92

areas, scopulae and opposite claws; Dibuninae have three areas, no scopulae and parallel claws. Zairebiantinae seem not to be a Biantidae because the eyes are placed on two distinct mounds close to each other and located in the middle of the cephalothorax (Kauri 1985) instead of far apart and near the line I. Unfortunately, the genitalia of *Zairebiantes microphthalmus* are poorly known and the drawing of Kauri (1985, fig. 249) is difficult to relate to any other family/subfamily of the Gonyleptoidea. There are no cladistic hypotheses for Biantidae subfamilies; but I believe that opposite claws and spindled metatarsi III are synapomorphic for the Stenostygninae. The presence of a membranous region ventrally in the ventral plate (Schwellkörper of Martens 1978, 1986) and the small number of articles in tarsi I (usually three) are synapomorphic for the Biantinae. The genitalia of the Dibuninae species are unknown. Members of the Stenostygninae have been recorded from the Antilles (Šilhavý 1973; Avram 1977), the Biantinae are recorded from the Oriental region (Roewer 1923; Martens 1978) and the Ethiopian region (Roewer 1923; Rambla 1982; Kauri 1985) and the Dibuninae from the Oriental region (Roewer 1923). *Stenostygnus pusio* is the first species of Biantidae recorded from Brazil, Colombia and Ecuador and is the second known representative of the family in South America. Gonzalez-Sponga (1992) recorded an unidentified species from Venezuela (specific locality not mentioned).

Stenostygnus pusio is closely related to the "Caribbiantinae" by presence of opposite claws and large number of articles on tarsi I; and it lacks the membranous region ventrally on ventral plate (plesiomorphic). Another synapomorphy of the Stenostygninae, male metatarsi III spindled, couldn't be observed in *S. pusio* because all males studied were without third legs.

The convergences between some Biantidae and some Stygnidae are remarkable. Those of note are the opposite claws (Stenostygninae, Heter-

ostygninae), scopulae with spatulate hairs (Biantinae, Stenostygninae, Heterostygninae), last tarsal article III–IV flattened (Stenostygninae, Heterostygninae), eye mound divided and situated back in the cephalothorax, dorsal scute rectangular/slightly elliptical, and pedipalpal coxae/femur/patella lengthened.

Based on the convergences mentioned (that are synapomorphic for Heterostygninae) and by the presence of male genitalia with slender ventral plate and posterior claws pectinated, the other genera and species formerly placed in the Stenostygninae are transferred to the Heterostygninae. *Stenostygnus magnus* Caporiacco will be the type species of a new genus of Heterostygninae (Pinto-da-Rocha unpubl. data).

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RESEARCH NOTES

REPORT ON A RARE DEVELOPMENTAL ANOMALY IN THE SCORPION, *CENTRUROIDES VITTATUS* (BUTHIDAE)

While perusing scorpion samples to delineate the distribution of *Centruroides vittatus* (Say) in the central United States, we discovered a specimen in the collection of the Emerson Entomological Museum of Oklahoma State University with two fully formed metasomas and telsons (Figs. 1, 2). This anomaly, involving complete duplication of the metasoma and telson, has been reported very rarely in the past. Although known in ancient times (see Vachon 1953), it was first described in the modern literature by Pavesi (1881) in the chactid, *Euscorpius germanus* (Koch). Duplicate metasomas and telsons have since been reported in *E. carpathicus* (Linnaeus) and in several buthids, including *Buthacus leptochelys* (Hemprich & Ehrenberg), *Androctonus crassicauda* (Olivier), *Hottentotta* (= *Buthotus*) *alticola* (Pocock), *Centruroides infamatus* (Koch), *C. gracilis* (Latreille), *C. margaritatus* (Gervais) and *C. exilicauda* (Wood) (= *C. sculpturatus* Ewing) (Berland 1913; Brauer 1917; Campos 1918; Franganillo 1934; Millot & Vachon 1949; Vachon 1953; Williams 1971; Armas 1977). In a few cases (i. e., in *E. germanus*, *B. leptochelys*, and *C. gracilis*), the duplication involves part of the mesosoma as well, with the bifurcation arising at the level of mesosomal segment III or IV. Brauer (1917) demonstrated that the condition results from splitting of the posterior part of the embryonic germ band. In his study of 5000 embryos of *E. carpathicus*, duplication-type anomalies appeared in 13 specimens; of these, only one (or 0.02%) involved potential duplication of the metasoma.
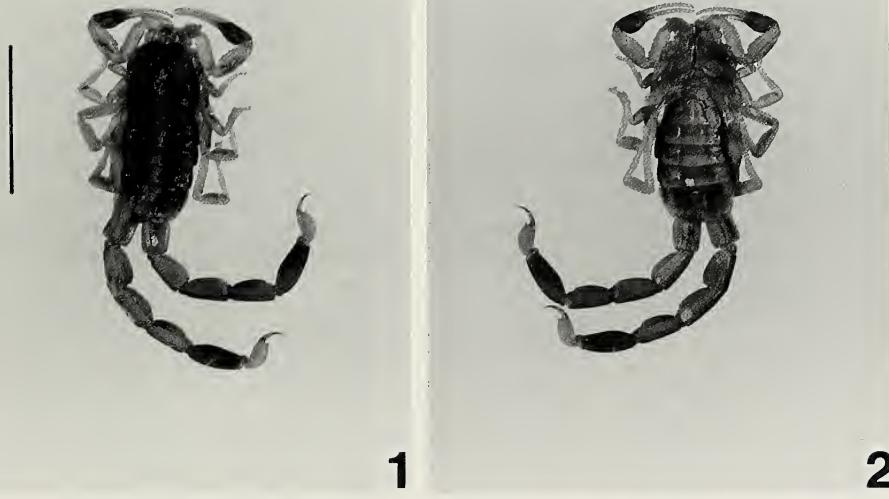
Figures 1, 2.—Anomalous specimen of *Centruroides vittatus*. 1, Dorsal view; 2, Ventral view. Scale line = 10 mm.
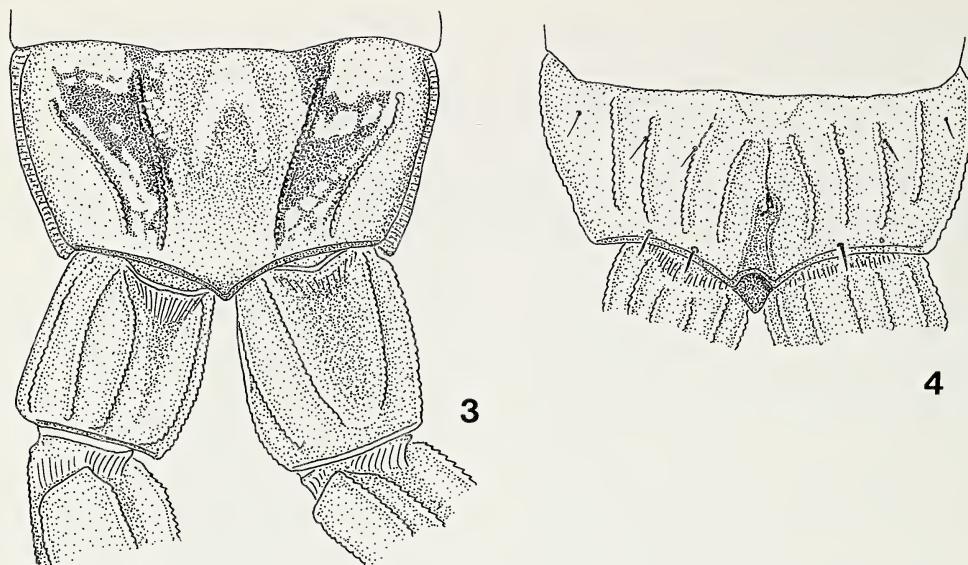
Figures 3, 4.—Mesosomal segment VII and proximal metasomal segments of anomalous *Centruroides vittatus*. 3, Dorsal view; 4, Ventral view.

The present specimen of *C. vittatus*, an immature female, most likely in the fifth instar, was collected by L. Feldick on 4 November 1988 at Kinta, Haskell County, Oklahoma. It is very similar to the specimens of *A. crassicauda*, *H. alticola*, and *C. gracilis* illustrated in Millot & Vachon (1949), Vachon (1953), and Armas (1977), respectively. It also generally matches the specimen of *C. exilicauda* described by Williams (1971). The two metasomas and telsons are fully formed and the carination of the metasomal segments is normal. Each metasoma bears an anus ventrally at the end of the fifth segment. It is quite probable that each metasoma and telson was fully functional.

The seventh mesosomal segment is quite abnormal, as would be expected in order for it to accommodate two metasomas. The tergite (Fig. 3) terminates posteriorly in a distinct triangular projection between the origins of the two metasomas. The lateral keels of the tergite are relatively normal, but the median keel is posteriorly bifurcate. The sternite is even more aberrant (Fig. 4). Its posteromedial margin bears a narrow, deep, concave indentation, and there is an irregularly-shaped boss and ridge along the posterior midline. This structure is flanked laterally by four pairs of keels (normal specimens have only four keels total – two submedians and two laterals – on the same sternite). Five pairs of setae are sym-

metrically placed on the sternite as shown in Fig. 4.

We thank D. C. Arnold, curator of the Emerson Entomological Museum, Oklahoma State University, for loan of the specimen and our wives for assistance with translating the literature. The photographs were taken by D. J. Lyons of the NCSM Exhibits Department; we are grateful for his efforts.

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W. David Sissom: Department of Biology & Geosciences, WTAMU Box 808, West Texas A & M University, Canyon, Texas 79016-0001 USA

Rowland M. Shelley: North Carolina State Museum of Natural Science, P.O. Box 29555, Raleigh, North Carolina 27626-0555 USA

DISPERSAL MECHANISMS OF *STEGODYPHUS* (ERESIDAE): DO THEY BALLOON?

Silk is used by spiders in dispersal in different ways. One method, bridging, is to cast a line into the breeze and, when it catches on a distant object, to climb out on the line to its end. Bridging may also be accomplished by dropping on a line and swinging on it to reach a new site (Barth et al. 1991). A second method is to balloon: when the extruded thread and the spider get enough lift from updrafts (usually thermals or vertical wind-velocity gradients), the spider will be lifted off the substrate and carried through the air (Decae 1986; Eberhard 1987; Greenstone 1990; Suter 1991, 1992; Weyman 1993; Follner & Klarenberg 1995).

Stegodyphus species (Eresidae) have been reported to disperse both by bridging and ballooning. Details of ballooning in *Stegodyphus* were reported by Wickler & Seibt (1986). They observed a gravid female *S. mimosarum*, one of three social species of *Stegodyphus*, ballooning over a distance of 18 m, having started at a height of 2 m. The spider had a body length of 10 mm with an estimated mass of 85–150 mg and was hanging from 3–4 silk threads of 60–80 cm length, i.e., the estimated total silk length was 1.8–3.2 m.

We compare the dispersal methods of bridging and ballooning for *Stegodyphus* in terms of their aerodynamics, consequences and relative importance. With this analysis we evaluate previous interpretations of dispersal of *Stegodyphus* in relation to current knowledge of their ecology and population biology. We use evidence from the literature and our own general observations made during several years of fieldwork with four species of *Stegodyphus*, namely, the social *S. dumicola* Pocock 1898 and *S. mimosarum* Pavesi 1883, and subsocial *S. lineatus* Latreille 1817 and *S. bicolor* (O. Pickard-Cambridge 1869).

We estimated the vertical air velocity required for Wickler & Seibt's (1986) *S. mimosarum* to remain airborne, using Suter's (1991) equation 7:

$$V_{sb} = W \div (11.5 \times L \times W^{0.094} + 1.94 \times W^{0.366})$$

where V_{sb} = vertical air velocity in m/sec acting on the spider's silk and body, W = weight in μN ($1\ \mu$N ≈ 0.1 mg), L = silk length in m. To apply this equation, we assumed that the physical parameters remain constant beyond the boundaries for which Suter's equation was developed. By substituting the maximum silk length and minimum *S. mimosarum* mass (above), a vertical velocity component of 9.2 m/s was necessary; minimum silk length and maximum spider mass requires 21.6 m/s. A wind of this strength would not have been described as a "barely perceptible breeze" (Wickler & Seibt 1986; p. 628), which may refer to a 0.1–1.0 m/s wind. A horizontal wind of 3 m/s near the ground is the maximum at which thermals, suitable for ballooning, can be maintained (Greenstone 1990; Weyman 1993). For controlled ballooning, we assume a maximum vertical wind component of 3 m/s, following Stull's (1988) description of boundary layer meteorology. If Wickler & Seibt's (1986) *S. mimosarum* experienced vertical winds of 0.1–3 m/s, it would have required 12–655 m of silk to become airborne.

It is possible that the drag line was longer than reported because its distal end can be difficult to see (Eberhard 1987). Furthermore, the above calculation does not take into account that spiders can change the drag on their bodies by several orders of magnitude when changing posture in relation to the direction of air flow (Suter 1992).

Wickler & Seibt's (1986) *S. mimosarum* was at least 3–6 times the maximum mass (25.5 mg) found in 2800 ballooning species investigated by Greenstone et al (1987). It clearly requires extreme conditions for this spider to experience lift. These conditions are well outside the boundaries used in aerodynamic models of spider ballooning (Humphrey 1987; Suter 1991, 1992). Ballooning is the domain of small spiders (Weyman 1993) and over 90% of them are < 1 mg in size (Greenstone et al. 1987). When members of large taxa, such as mygalomorphs, balloon, it is the small spiderlings (< 2.2 mg with an outlier of 5.8 mg) that do so (Coyle et al. 1985).

Social *Stegodyphus* are typically big at first dispersal, as they usually disperse only when adult, or, more rarely, subadult. Dispersing female *S. dumicola* weigh 103–213 mg and males some 23–48 mg (Henschel et al. 1995). By contrast, sub-

social *S. lineatus* are 3–8 mg at first dispersal (Schneider 1992), within the size range of some heavy ballooning spiders. Nonetheless, *S. lineatus* have not been recorded ballooning.

On three occasions, one of the authors (JH) observed *S. dumicola* parachuting downwards when his presence disturbed spiders that were casting silken lines, evidently for bridging. The spiders landed several meters away on the ground. Size may explain why airborne *Stegodyphus* drop and land a short distance from the start. Perhaps other observations of ballooning by *S. dumicola* (in the laboratory, S. Kürpick pers. comm.) and by *S. sarasinorum* Karsch (Jambunathan 1905; Jacson & Joseph 1973) also occurred upon disturbance caused by the observers' presence. If escape were not the case, the observation of several *S. sarasinorum* ballooning together on one gossamer (Jacson & Joseph 1973) would be puzzling in view of the weight handicap this imposes on the conditions for remaining airborne.

We have seen *Stegodyphus* casting bridging lines on numerous occasions over distances of several meters. The slightest vertical air movement is sufficient for silken threads to be airborne (Suter 1991). Thus, silken threads easily cross gaps, enabling even large spiders to move on them when the lines snag on objects. Bridging was used by over 88% of the dispersing *S. dumicola* recorded by Henschel (pers. obs.).

The adoption of the tiptoe posture and the location of nests on the windward side of trees were interpreted as indirect indications of aerial dispersal (Wickler & Seibt 1986; Seibt & Wickler 1988). However, we have observed *Stegodyphus* standing tiptoe when casting bridging lines and reaching windward destinations via these bridging lines. This stance and location can therefore not serve as independent evidence of dispersal by ballooning.

Both social and subsocial species of *Stegodyphus* appear to face high risks of predation during dispersal (Ward & Lubin 1993; Henschel pers. obs.). Ballooning must be regarded as a hazardous method of dispersal for such slow-moving spiders that are ungainly off the web. By ballooning, they immediately forgo the possibility of backtracking to the safety of their colony of origin if the new site turns out to be unsuitable, especially if it is occupied by predators such as ants. For this reason, bridging is likely to be safer.

Occasionally, social spiders are carried to new sites by agents beyond their control. Storms translocate spiders, large potential prey escape with spiders attached, mammals and birds pass through webs bearing spiders, and Gabar goshawks carry occupied spider nests onto their own nests (Seibt & Wickler 1988; Henschel et al. 1992a, b; Riechert & Roeloffs 1993). Social spiders may colonize new regions by such fortuitous, hazardous translocations, but the significance at the population level is unknown.

The extreme population subdivision indicated by protein allozyme electrophoresis (Smith & Engel 1994) constitutes additional evidence that *Stegodyphus* have poor powers of dispersal. Colonies of *S. sarasinorum* in India had low frequencies of polymorphic loci with most of the variation occurring between different subpopulations. The known distances of dispersal of *Stegodyphus* during their lifetime are short: 1–26 m for *S. dumicola* (Henschel pers. obs.); 1–83 m for *S. lineatus* (Ward & Lubin 1993). Most *Stegodyphus* disperse no more than a few meters at a time (op. cit.; Schneider 1992). Furthermore, the patchy distribution patterns of webs suggests that most dispersal is over very short range (Wickler 1973; Seibt & Wickler 1988; Schneider 1992; Ward & Lubin 1993; Henschel pers. obs.).

We conclude that there is insufficient evidence to support the impression expressed by authors citing the Wickler & Seibt (1986) report (e. g., Seibt & Wickler 1988; Riechert & Roeloff 1993; Smith & Engel 1994; Avilés 1995) that *Stegodyphus* uses ballooning regularly and therefore is expected to have greater powers of dispersal than other social spiders. Current evidence indicates that *Stegodyphus* are conservative dispersers that normally employ bridging lines to move only short distances from their natal nest. Rarely, spiders may become airborne when they are disturbed and drop while casting bridging lines. They escape and land a short distance away, no further than when bridging.

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Joh R. Henschel: Desert Ecological Research Unit of Namibia, P.O.Box 1592, Swakopmund, Namibia

Jutta Schneider: Max-Planck-Institut für Verhaltensphysiologie, Seewiesen, D-82319 Starnberg, Germany

Yael D. Lubin: Mitrani Centre for Desert Ecology, Blaustein Institute for Desert Research, Ben Gurion University of the Negev, 84993 Sede Boqer Campus, Israel

DISPERSAL AGGREGATION OF *SPHODROS FITCHI* (ARANEAE, ATYPIDAE)

Observations of dispersal aggregations of mygalomorph spiderlings have been rarely reported in the literature. Spiderlings of the European purseweb, *Atypus affinis* Eichwald 1830 (Atypidae), were discovered climbing up vegetation on warm, spring days (Bristowe 1939). As several reached the top of a garden stake, the wind dislodged them and their draglines, which became attached to other objects. The young of another species of purseweb spider, *Sphodros rufipes* (Latreille 1829), performed similar preballooning behavior in the laboratory (Muma & Muma 1945). Coyle (1983) was fortunate in observing the dispersal of purseweb spiderlings in North Carolina. *Sphodros fitchi* Gertsch & Platnick 1980 is a purseweb spider found in the central plains states from Nebraska to Oklahoma and Arkansas (Gertsch & Platnick 1980). It appears to be the rarest of three species of *Sphodros* which occur in northeastern Kansas. Therefore, the natural history information of *S. fitchi* is limited to a few anecdotal observations (Fitch 1963; Guarisco 1988; Morrow 1985; Teeter 1984). This is the first report of a dispersal aggregation of spiderlings of this species.

At noon on 2 April 1995, a dispersal aggregation of immature *Sphodros fitchi* was discovered by the first author in the highest branches of a 1 m tall eastern red cedar (*Juniperus virginiana* L.) on the west campus of the University of Kansas in Douglas County, Kansas. The small tree was located at the edge of a lawn and second growth woods composed predominantly of osage orange trees (*Maclura pomifera* (Raf.) Schneid.) 3–5 m in height. A group of 14 immatures and two dense, silk mats, each 1 cm² in area, were seen on the tips of two branches. During 30 minutes of observation, the spiders slowly walked on the silk mats and the silk strands between the branches and the adjacent branch tips. Four appeared to let go, fell a few centimeters on draglines to lower branches, then slowly climbed back to the top. Ballooning behavior in *Sphodros* and other mygalomorphs consists of descending on a dragline until the force of the wind breaks it near its attachment point. Then the spider and dragline are carried by the breeze (Coyle 1983). Therefore, the four observations may represent unsuccessful ballooning attempts. The sky was partly cloudy, the temperature was about 23 °C, and there were westerly gusty winds.

Later that day, we returned to the site, and the second author discovered a large, white silk tube attached to the base of the red cedar tree. No spiderlings were observed. The tube and the cedar trunk were each approximately 2.5 cm in diameter. The tube extended 17 cm up the side of the tree. The next day, the silk tube was excavated and it contained an adult *S. fitchi* female. No egg-sac or egg remains were found inside the tube, which was 33.5 cm in total length. The length of the female, including chelicerae, was 2.7 cm. The lengths of five spiderlings from the dispersal aggregation, including chelicerae and spinnerets, ranged from 2.25–2.50 mm. The average width of the prosoma at the anterior edge was 0.68 mm ($n = 5$, range 0.60-0.76). Two of the immatures were placed in vials containing moist soil and vertical twigs. Small silk tubes covered with soil particles were discovered the next day. One was located on the side of the vial and the second was located along a twig. The aerial portion of each tube was about 1 cm in length. The following day, the web along the twig was 2 cm in length.

The dispersal aggregation described here resembles those described by other authors. Although no actual ballooning was witnessed, the behavior of four spiderlings was consistent with that described by Coyle (1983). The immatures were capable of independent living, based on the construction of their own webs in captivity.

We would like to thank Dr. Hampton Shirer, Lawrence, Kansas for temperature information.

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Bruce Cutler: Electron Microscopy Laboratory, and Department of Entomology, University of Kansas, Lawrence, Kansas 66045-2106 USA.

Hank Guarisco: Kansas Biological Survey, 2041 Constant Avenue, Lawrence, Kansas 66047 USA.

PREDATION BY *MISUMENOPS ASPERATUS* (ARANEAE, THOMISIDAE) ON THE METALLIC PITCH NODULE MOTH, *RETINIA METALLICA* (LEPIDOPTERA, TORTRICIDAE)

Forest entomologists have long suspected that spiders play important roles in the population dynamics of forest insects because of their predatory habits and abundance on trees (e. g., see Loughton et al. 1963). Despite this potential importance, however, few observations of spiders actually feeding on tree pests have been reported. Some exceptions include spiders observed preying on destructive bark beetles (Jennings & Pase 1975) and on forest-tree defoliators (Jennings & Houseweart 1989). Possible reasons for the scarcity of observed predatory bouts by spiders in forests and tree plantations include: (1) the diminutive size of spiders compared to the tree; (2) the cryptic habits of some spiders, especially those that employ hunter-ambusher tactics; and (3) the low prey-capture success of some species (Jackson 1977). Hunting spiders are less apt to be observed with prey than web-spinners. Large orb weavers and other web-spinners that "store" prey in their webs offer an easier means of prey assessment. Nentwig (1987) noted that nonweb-building spiders handle only one prey at a time; consequently, their hunting success is relatively low, and ingestion time short. Hence, a low percentage of hunting spiders are found with prey at any specific time in a population (Nentwig 1987).

Here we describe predation by an ambushing crab spider on a destructive insect pest of ponderosa pine, *Pinus ponderosa* (Laws.), in a shelterbelt of Nebraska. This is the first recorded instance of spider predation on the metallic pitch nodule moth, *Retinia metallica* (Busck), in North America. Larvae of this moth bore into the new growth of pine stems, twigs, and branches (Furniss & Carolin 1977; Dix et al. 1986). During July, the larvae produce a nodule or lump of pitch and frass at the point of attack. Such feeding stunts tree growth and frequently kills the tips. Heavily infested trees have excessive branching.

On 22 May 1987, the senior author observed a crab spider feeding on a small female moth near the apex of a ponderosa pine branch (1.2 m high). The tree was approximately 5 m high and was growing in a multi-row farmstead shelterbelt

(Hollst Farm) near Mead, Saunders County, Nebraska (41°16′N, 96° 28′W). The spider with captured prey was collected, photographed (Fig. 1), and then preserved in 70% ethanol for later identification.

The crab spider, an adult female *Misumenops asperatus* (Hentz), was identified by the junior author. The specimen will be deposited in the arachnid collections of the U. S. National Museum of Natural History, Washington, D. C.

This species of crab spider hunts by stealth and ambush (Gertsch 1939). Branch apices are hunting sites where these crab spiders can wait for flying insects such as moths to land (pers. obs.). Because *R. metallica* moths frequent branch apices and similar microhabitats, they are susceptible to predation by ambushing crab spiders like *M. asperatus*. However, the frequency and extent of predation by *M. asperatus* on *R. metallica* are unknown. This insect, and similar lepidopterous species whose larvae live inside the twigs of trees, is most susceptible to predation by spiders during the moth-flight period. In the collection locale, the adult flight of *R. metallica* spans three weeks during May and early June (Dix unpubl. data).

We suspect that hunting spiders are more successful at capturing small moths like *R. metallica* than are web-spinners. Moth scales provide a means of escape from spider webs (Eisner et al. 1964); however, such defenses are ineffectual against ambushing crab spiders. Juillet (1961) found that wandering spiders of the families Salticidae and Thomisidae killed three times as many adults of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.), as did web spinners of the family Araneidae.

Although *M. asperatus* is common on young ponderosa pines in Nebraska shelterbelts, the density of its populations on shelterbelt trees is unknown. It is found in both old field (e. g., Berry 1970) and arboreal habitats. In South Carolina, *M. asperatus* preyed on both larvae and adults of the Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock), another destructive insect pest of pine plantations (Eikenbary & Fox 1968).
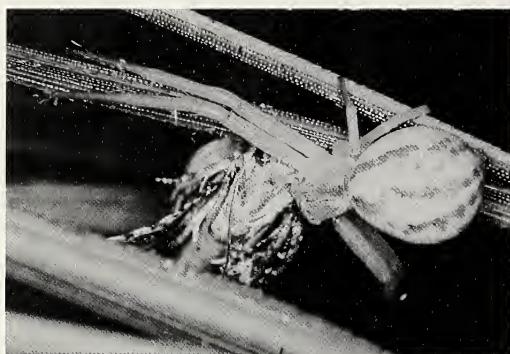
Figure 1.—A female *Misumenops asperatus* feeding on the metallic pitch nodule moth, *Retinia metallica*, on a ponderosa pine tree in Nebraska.

Ponderosa pine may gain some protection from the predatory habits of spiders like *M. asperatus*. Such mortality would be particularly important when spiders and other predators kill gravid moths of *R. metallica*. No doubt other spider species also capture and feed on *R. metallica*; however, this potential source of moth mortality has not been fully investigated. Similar observations of spider predation on other insect pests of ponderosa pine (e. g., scarab beetles (Jennings 1974), Southwestern pine tip moth (Jennings 1975; Lawson et al. 1983), and pine butterfly (Jennings & Toliver 1976)) support our conclusion.

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Mary Ellen Dix: Rocky Mountain Forest and Range Experiment Station, National Agroforestry Center, East Campus, University of Nebraska, Lincoln, Nebraska 68583-0822 USA

Daniel T. Jennings: Northeastern Forest Experiment Station, 180 Canfield Street, Morgantown, West Virginia 26505 USA

ON MALES OF CALIFORNIAN *TALANITES*
(ARANEAE, GNAPHOSIDAE)

Shortly after the revision of the North American species of *Talanites* (Platnick & Shadab 1976, as *Rachodrassus*), we discovered two additional species in California. These were recently described by Platnick & Ovtsharenko (1991), as *T. moodyae* and *ubicki*, on the basis of females. Here we report the newly discovered males.

One noteworthy observation on these specimens is the presence of a ventroapically projecting process at the base of the embolus (Figs. 2, 4). This process is not recorded for the species described in the above papers, and we were unable to observe it in specimens of *T. echinus* (Chamberlin) or *exlineae* (Platnick & Shadab). The Californian *Talanites* have already been shown to be somatically distinct in having unusually small eyes (Platnick & Ovtsharenko

1991). Perhaps these character states are derived. However, given that the Californian fauna is rife with relictual arachnids, plesiomorphy cannot be completely ruled out. In fact, the two species have a typically relictual distribution pattern and, despite an intense collecting effort by the authors, are known from only a few localities. (Given the rarity of the species, we list below all of their known localities.) The *Talanites* species from the eastern United States and Mexico, in contrast, are each much more widely distributed, showing a combined range from San Luis Potosí and Texas to Florida, north to Arkansas and Virginia.

Following the format in the above papers we describe here the males of the two species. The unique male specimens have been deposited at the California Academy of Sciences (CAS), other
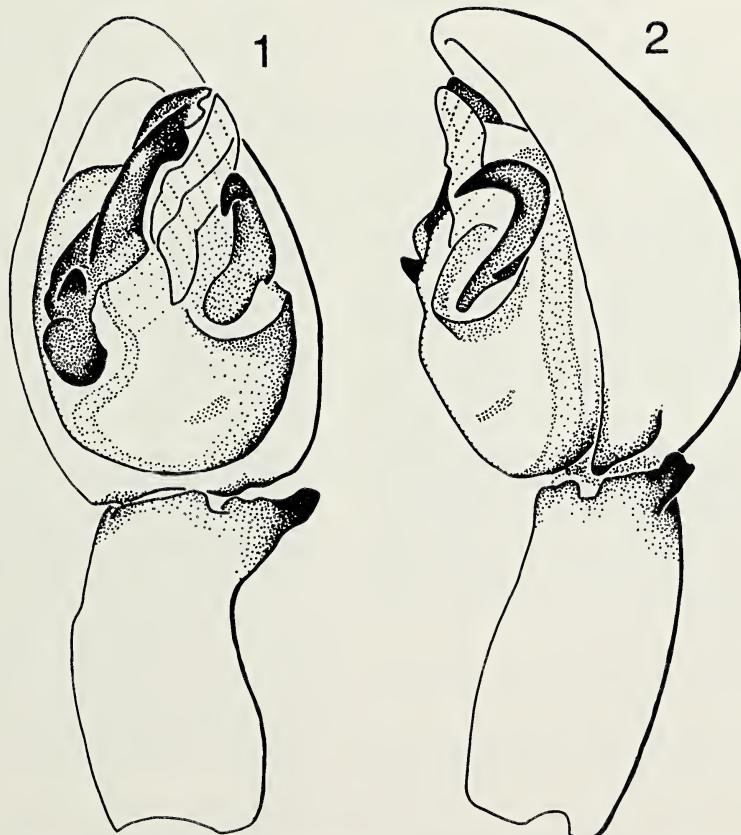
Figures 1–2.— *Talanites moodyae* Platnick & Ovtsharenko. 1, Left male palp, ventral view. 2, Same, retrolateral view. (setae omitted)
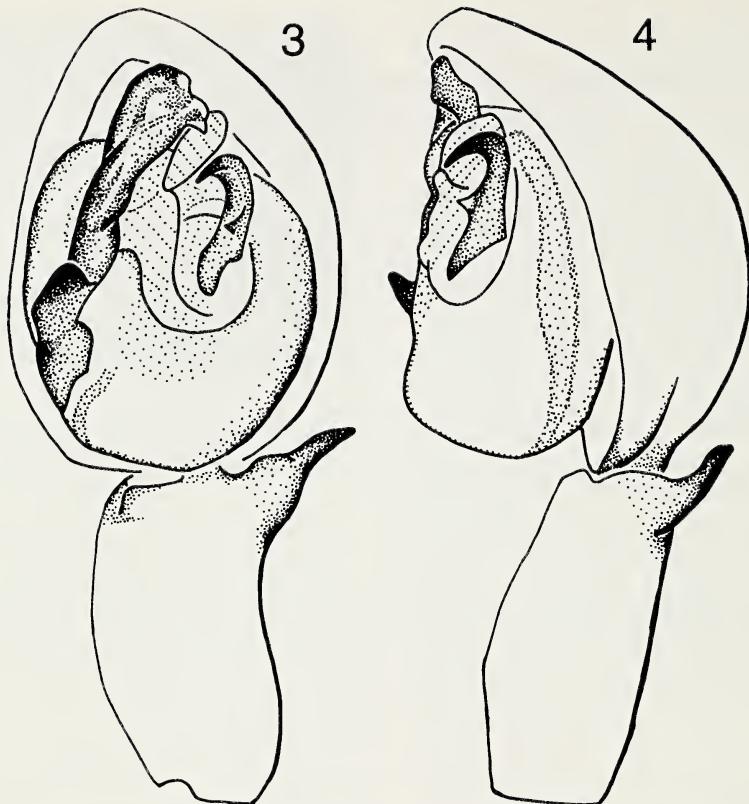
Figures 3–4.—*Talanites ubicki* Platnick & Ovtsharenko. 3, Left male palp, ventral view. 4, Same, retrolateral view. (setae omitted)

specimens are in the collections of the American Museum of Natural History (AMNH), California Department of Food and Agriculture (CDFA), and D. Ubick (CDU). We thank Charles E. Griswold of the California Academy of Sciences and Norman I. Platnick of the American Museum of Natural History for reading and commenting upon an earlier draft of this paper. Special thanks go to Joy Boutin and Bill Tyson for helping collect specimens of *Talanites*; Joy Boutin also assisted in rearing the males of *T. ubicki*. We thank the California Department of Food and Agriculture for helping defray the publication costs. All measurements are in mm.

Talanites moodyae Platnick & Ovtsharenko
Figs. 1,2

Talanites moodyae Platnick & Ovtsharenko 1991: 119, figs. 15, 16 (female holotype in AMNH, not examined).

Diagnosis.—Males are distinguished from all other North American *Talanites* by the combined presence of a ventroapically directed pro-

cess on the embolar base, a small second point on the median apophysis, and reduced eyes.

Description.—*Male*: Total length 7.1. Carapace length 3.4; width 2.7. Femur II length 2.6. Eye sizes and interdistances: AME 0.08, ALE 0.09, PME 0.05 × 0.07, PLE 0.06 × 0.08, AME-AME 0.07, AME-ALE 0.08, PME-PME 0.15, PME-PLE 0.15, ALE-PLE 0.08, MOQ length 0.22, front width 0.21, back width 0.26. Leg spination: femora: I,IIp0-1-2, d1-1-1, r1-1-1; IIIp0-1-1, d1-1-1, r1-1-1; IVp1-1-1, d1-1-1, r1-1-1; tibiae: Ip1-1-1, v2-2-2, r1-1-2; IIp1-1-1, v2-2-2, r2-1-1; metatarsi: IIIp2-2-2, v2-2-2, r1-1-1. Palpal tibial apophysis flattened, directed retrolaterally; embolus distally pointed with ventroapically directed basal process; median apophysis with small, basal second point.

Female: Described by Platnick & Ovtsharenko (1991).

Material examined.— USA. **California:** *Fresno County:* Granite Hill, 1.5 mi NE Navelencia, 1 February 1994 (W. H. Tyson, CDFA), 1 juvenile. E slope Smith Mountain, 4 mi E Reedley,

grassland, under granite, 29 March 1991 (D. Ubick, CDU), 5 juveniles. 19 January 1994 (W. H. Tyson, CDFA), 2 females. *Tulare County:* S slope Smith Mountain, under serpentine, 19–21 January 1994 (W. H. Tyson, CDFA), 5 females, 19 juveniles. Bacon Hill, 5 February 1992 (M. J. Moody, CAS), 1 male. Twin Buttes, 2 December 1993 (W. H. Tyson, CDFA), 1 juvenile. Venice Hills, 12 March 1991, under rocks (W. H. Tyson, CDFA), 1 juvenile. Rocky Hill, E of Exeter on Hwy 130, grassland, under serpentine, 26 January 1991 (D. Ubick, CDU), 1 penultimate female.

Notes.—Three penultimate males were placed in a 10 × 8.5 cm plastic jar containing soil to a depth of 3 cm. The soil was maintained moist and a piece of cardboard was placed to provide cover. The spiders were fed termites; two of the spiders died, the third matured by 3 June 1992.

Talanites ubicki Platnick & Ovtsharenko
Figs. 3, 4

Talanites ubicki Platnick & Ovtsharenko 1991: 120, figs. 3, 4 (female holotype in AMNH, not examined).

Diagnosis.—Males are distinguished from all other North American *Talanites* by the combined presence of a ventroapically directed process on the embolar base, a large second point on the median apophysis, and reduced eyes.

Description.—*Male:* Total length 4.6. Carapace length 2.1; width 1.7. Femur II length 1.6. Eye sizes and interdistances: AME 0.05, ALE 0.09, PME 0.05 × 0.07, PLE 0.05 × 0.08, AME-AME 0.05, AME-ALE 0.04, PME-PME 0.08, PME-PLE 0.08, ALE-PLE 0.04, MOQ length 0.17, front width 0.15, back width 0.21. Leg spination: femora: Ip0-1-2, d1-1-1, r0-1-0; IIp0-1-1, d1-1-1, r0-1-0; III,IVp1-1-1, d1-1-1, r0-1-1; tibiae: I, IIp1-1-1, v2-2-2, r1-1-1; metatarsi: IIIp1-1-1, v2-2-2, r1-1-1. Palpal tibial apophysis pointed, directed retrodorsally; embolus distally broad with ventroapically directed basal process; median apophysis with large second point.

Female: Described by Platnick & Ovtsharenko (1991).

Material examined.—USA. **California:** *Marin County:* Novato, San Marin Drive, 18 April 1992 (D. Ubick & J. Boutin, CAS), 1 male. December to March 1982–1992 (D. Ubick, CDU), females and juveniles.

Notes.—The male specimen was one of four penultimate males collected at the type locality, a serpentine grassland on the SW slope of Burdell Mtn. just north of Simmons Lane, Novato. (The correct spelling of the type locality is Novato, not "Novata" as given by Platnick & Ovtsharenko 1991.) The *Talanites* were found under large serpentine floats at the edge of a seepage where the soil conditions were moist. In the lab, the spiders were placed in terraria on moist serpentine soil clumps. A variety of insect prey was introduced during the captivity. The spiders were reluctant feeders but were observed feeding on embiids, termites, and *Drosophila.* Of the four spiders, two died without molting, one died during molting in late May, and one molted successfully on 30 May 1992.

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Darrell Ubick: Associate, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118 USA.

Marjorie J. Moody: Entomologist, California Department of Food and Agriculture, P. O. Box 3468, Visalia, California 93278 USA.

CHEMICAL ATTRACTION OF MALE CRAB SPIDERS (ARANEAE, THOMISIDAE) AND KLEPTOPARASITIC FLIES (DIPTERA, MILICHIIDAE AND CHLOROPIDAE)

After the first day of a study testing the attraction of scavenging flies (Diptera, Milichiidae and Chloropidae) to defensive chemicals of true bugs (Heteroptera), it was apparent that males of one type of crab spider (Thomisidae) were also attracted to the chemical treatments. Therefore, the original goal of the study was abandoned in 1993 in favor of a full-time investigation of spider attraction.

Traps were constructed of transparent cylindrical containers (20.2 × 19.7 cm; Tri-State Molded Plastic, Dixson, Kentucky) by cutting two 9-cm diameter holes in opposite sides, and covering each hole with an inwardly projecting screen funnel (Aldrich et al. 1984). On 8 June 1993, nine traps were hung from stakes in a 0.9 ha fallow field 10 m apart in contact with foliage (mixed grasses, goldenrod, and bush-clover), alternating the following three treatments: *(E)*-2-octenal, *(E)*-2-decenal, and unbaited controls. Chemicals were dispensed from cotton swabs (Q-Tips®, Chesebrough Pond's Co., Greenwich, Connecticut) dipped in neat standards (*ca.* 200 μl; Bedoukian Research, Inc., Danbury, Connecticut). Traps were inspected every 1–2 days, and rebaited every 2–3 days.

From 9–18 June, 200 males of *Xysticus ferox* (Hentz) (Thomisidae) were caught in traps baited with alkenals; none were captured in controls (Table 1, Field 1). Capture of *X. ferox* males was variable for both *(E)*-2-octenal-baited traps (totals of 28, 33, 59 males/trap) and *(E)*-2-decenal-baited traps (7, 28, and 45 males/trap) such that attraction to *(E)*-2-octenal was not significantly greater than to *(E)*-2-decenal ($P = 0.33$).

From 18–20 June 1993, captures of *Xysticus* males dropped to almost zero in Field 1; therefore, on 21 June the traps were redeployed in another field (0.5 ha) that had been lightly sown with a mixed ground cover including red clover and vetch (Table 1, Field 2). Vegetation in Field 2 was sparse, so traps were placed directly on the ground. From 22 June–15 July, a total of 74 males of four *Xysticus* spp. was caught in traps baited with *(E)*-2-octenal or *(E)*-2-decenal: *X. ferox, X. discursans* Keyserling, *X. triguttatus* Keyserling, and *X. auctificus* Keyserling. No *Xys-*

ticus females were caught, and one *Xysticus* individual was caught in a control trap. *Xysticus* spp. from Field 2 were grouped because we could not reliably separate the species; however, 15 out of the 25 specimens determined were *X. auctificus*. Again, the attraction to *(E)*-2-octenal was greater, but not significantly so, than to *(E)*-2-decenal (Table 1, $P = 0.35$).

In order to determine if other compounds were involved in spider attraction or if the known attractants acted synergistically, additional sets of traps were deployed in Field 2 baited in a similar manner with *(E)*-2-octenoic acid, octanoic acid, 1-octanol, *(E)*-2-octenal/*(E)*-2-decenal (1:1 blend), *(E)*-2-nonenal, *(E)*-2-decenal acetate, and *(E)*-2-hexenal butyrate (Aldrich Chemical Co., Milwaukee, Wisconsin; or Bedoukian Research, Inc.). Standards of octenal and decenal contained impurities of the corresponding acids (1.48% *(E)*-2-octenoic acid; 1.58% *(E)*-2-decenoic acid; analyzed by standard methods, e. g., Aldrich et al. 1984), and the acids predominated in extracts of Q-Tips after 24 h field exposure in hot, sunny weather (88% and 65% *(E)*-2-octenoic acid and *(E)*-2-decenoic acid, respectively). Nevertheless, there was no indication that *(E)*-2-octenoic acid or octanoic acid are attractive to *Xysticus* species. Octanol was a common minor impurity ($< 1\%$) in both octenal and decenal standards, but it seemed inactive. Similarly, there was no indication of synergism between octenal and decenal, no evidence that *(E)*-2-nonenal is attractive, and common esters of stink bugs, *(E)*-2-decenyl acetate, and plant bugs (Miridae), *(E)*-2-hexenyl butyrate, appeared inactive.

In 1994, traps were deployed earlier in Field 1 (14 May–30 June), and an additional set of traps was baited with another alkenal commonly produced by heteropterans, *(E)*-2-hexenal (Bedoukian Research, Inc.) (Aldrich 1988). *Xysticus* individuals were caught from the first day of the experiment in numbers greater than the previous year (Table 1). The results for *Xysticus* (identified to genus only) corroborated previous results for male-specific attraction to *(E)*-2-octenal and *(E)*-2-decenal, but *(E)*-2-hexenal was not attractive.

In 1994 we also decided to collect the trapped

Table 1.—Total numbers of *Xysticus* species males and females caught in traps in 1993 and 1994. Within a column, sums followed by the same letter are not significantly different at the 5% level (three traps/treatment; one-way ANOVA of rank transformed sums/trap/trapping period, fit separately for each field).

| | 1993 | | | | 1994 | |
| | Field 1 | | Field 2 | | Field 1 | |
Treatment	Male	Female	Male	Female	Male	Female
(*E*)-2-Hexenal	—	—	—	—	1a	3a
(*E*)-2-Octenal	120a	0a	52a	0a	224b	0a
(*E*)-2-Decenal	80a	0a	22a	0a	115b	1a
Control	0b	0a	1b	0a	0a	0a

milichiid and chloropid flies, several of which are kleptoparasitic on true bugs caught in spider webs (Eisner et al. 1991; Landau & Gaylor 1987). Exclusively females of one milichiid, *Milichiella arcuata* (Loew), were significantly attracted to *(E)*-2-hexenal-baited traps, but not to the other alkenal-baited or control traps (Table 2). Fifteen chloropid species were caught, totalling 2269 individuals (predominantly females), but *Ocella trigramma* (Loew) accounted for over 95% of the total, with *O. cinerea* (Loew) and *O. parva* (Adams) comprising about 1%. Chloropids were attracted to all three alkenals compared to control traps; however, *(E)*-2-octenal was most attractive, followed by *(E)*-2-decenal, and *(E)*-2-hexenal was the least attractive (Table 2). These data suggest that scavenging milichiid and chloropid flies use allomones from dying bugs in spider webs (and probably elsewhere), not just to find food, but also to discriminate between heteropteran species (see also Sugawara & Muto 1974).

The surprising discovery that male *Xysticus* species are attracted to *(E)*-2-octenal and *(E)*-2-decenal is difficult to explain. *Xysticus* species chemically attracted to alkenals are brown, ground-dwelling spiders that probably seize most of their prey after laying-in-wait in the litter zone (Morse 1983). A variety of heteropterans are among the natural prey of litter-inhabiting crab spiders (Nyffeler & Breene 1990; Nentwig 1986; Araya & Haws 1988); therefore, it is possible that *Xysticus* use alkenals as host-finding kairomones as do scavenging flies. This seems unlikely, though, because Heteroptera constitute only a small portion of the prey taken by ground-dwelling *Xysticus* species (Nyffeler & Breene 1990; Nentwig 1986), and esters of Heteroptera were unattractive. Most importantly, only four females and no immatures were caught in chem-

ically baited traps, compared to 615 adult *Xysticus* males.

Behavioral studies have shown that both web-building and hunting spiders communicate with pheromones (Barth 1993; Pollard et al. 1987; Rovner 1991; Suter & Hirscheimer 1986; Tietjen 1979). To date, there has been only one spider sex pheromone chemically identified: unmated females of the sheet-web weaving spider, *Linyphia triangularis* (Clerck) (Linyphiidae), deposit the dimer of *(R)*-3-hydroxybutyric acid on their webs which, after breaking down to the more volatile monomer, elicits the web reduction behavior of males leading to copulation (Schulz & Toft 1993). Discovery of an acidic pheromone for a spider suggested that acidic impurities in alkenal standards might be responsible for attraction of *Xysticus* males. Nonetheless, traps baited with high and low (10 μl) doses of *(E)*-2-octenoic acid were unattractive in the field.

In summary, the exact role of (*E*)-2-decenal and (*E*)-2-octenal in attraction of *Xysticus* males is not yet clear, but our results suggest that the alkenals, or impurities in the synthetic standards, are related or identical to sex pheromone components of these spiders. This is apparently the

Table 2.—Milichiid and chloropid flies caught in traps in 1994. Within a column, sums followed by the same letter are not significantly different at the 5% level (three traps/treatment; one-way ANOVA of rank transformed sums/trap/trapping period).

Treatment	Milichiidae	Chloropidae
(*E*)-2-Hexenal	136a	33a
(*E*)-2-Octenal	1b	2069b
(*E*)-2-Decenal	7b	167c
Control	0b	0d

first report of spiders being attracted into traps baited with synthetic chemicals.

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Jeffrey R. Aldrich: Insect Chemical Ecology Laboratory, USDA-ARS, Bldg 007, Agricultural Research Center-West, Beltsville, Maryland 20705 USA

Tev M. Barros: Department of Entomology, University of Maryland, College Park, Maryland 20742 USA

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33, dorsal views; 28, 30, 32, 34, prolateral views of moveable finger; 27, 28, *A-us x-us,* holotype male; 33, 34, *A-us y-us,* male. Scale = 1.0 mm.

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