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**OBSERVATIONS ON THE NATURAL HISTORY OF
SPHODROS ABBOTI AND *SPHODROS RUFIPES* (ARANEAE, ATYPIDAE),
WITH EVIDENCE FOR A CONTACT SEX PHEROMONE**

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ABSTRACT

The three populations of *S. abboti* studied exhibit much higher densities than the two of *S. rufipes*. In *S. abboti* mating occurs in July, egg laying in August, hatching in September, and the fully equipped and self-sufficient third instar spiderlings develop by November. The tubes of *S. abboti* are proportionately longer and have a greater aerial length to underground length ratio than do those of *S. rufipes*. Other differences in tube architecture exist. Both species capture and feed upon a wide variety of ground arthropods and discard prey remains through the upper end of the tube. *S. abboti* males search for mates in daylight and appear to be generalized wasp-ant mimics. Our observations of *S. abboti* male behavior suggests that adult female tubes are marked by a contact sex pheromone.

INTRODUCTION

Despite their covert behavior and patchy abundance, purse-web spiders (Atypidae) have attracted considerable attention from araneologists for at least two reasons. First, atypids possess an interesting mixture of primitive and specialized characteristics, their outstanding specializations being part of a unique strategy of capturing prey through the walls of a silk tube, the purse-web. Secondly, these spiders are found in north temperate zone countries where other mygalomorph taxa are poorly represented but where araneologists are relatively abundant. Major contributions toward understanding the natural history of European *Atypus* species have come from Enock (1885, 1892), Bristowe (1933, 1958), Ehlers (1937), Gerhardt (1929, 1933), Clark (1969), and Kraus and Baur

(1974). Knowledge of North American *Sphodros* species is based primarily upon the observations of McCook (1888), Poteat (1890), Gertsch (1936, 1949, 1979), Muma and Muma (1945), Bishop (1950), and Gertsch and Platnick (1980).

In order to learn more about *Sphodros* behavior and ecology, we spent seven days in 1973 (July 15 to 19 and October 5 and 6) observing *Sphodros abboti* Walckenaer and *Sphodros rufipes* (Latrielle) populations at five localities. *S. abboti* was studied at Millpond Plantation on the edge of Thomasville, Thomas Co., Georgia; at Suwannee River State Park, Suwannee Co., Florida, and at Mud Springs, near the Welaka Reserve of the University of Florida, Putnam Co., Florida. *S. rufipes* was observed at Florida Caverns State Park, Jackson Co., Florida, and at Torreya State Park, Liberty Co., Florida. In this paper we present and discuss these observations if they extend or clarify earlier observations, if they affect existing hypotheses, or if they break new ground.

SPHODROS ABBOTI

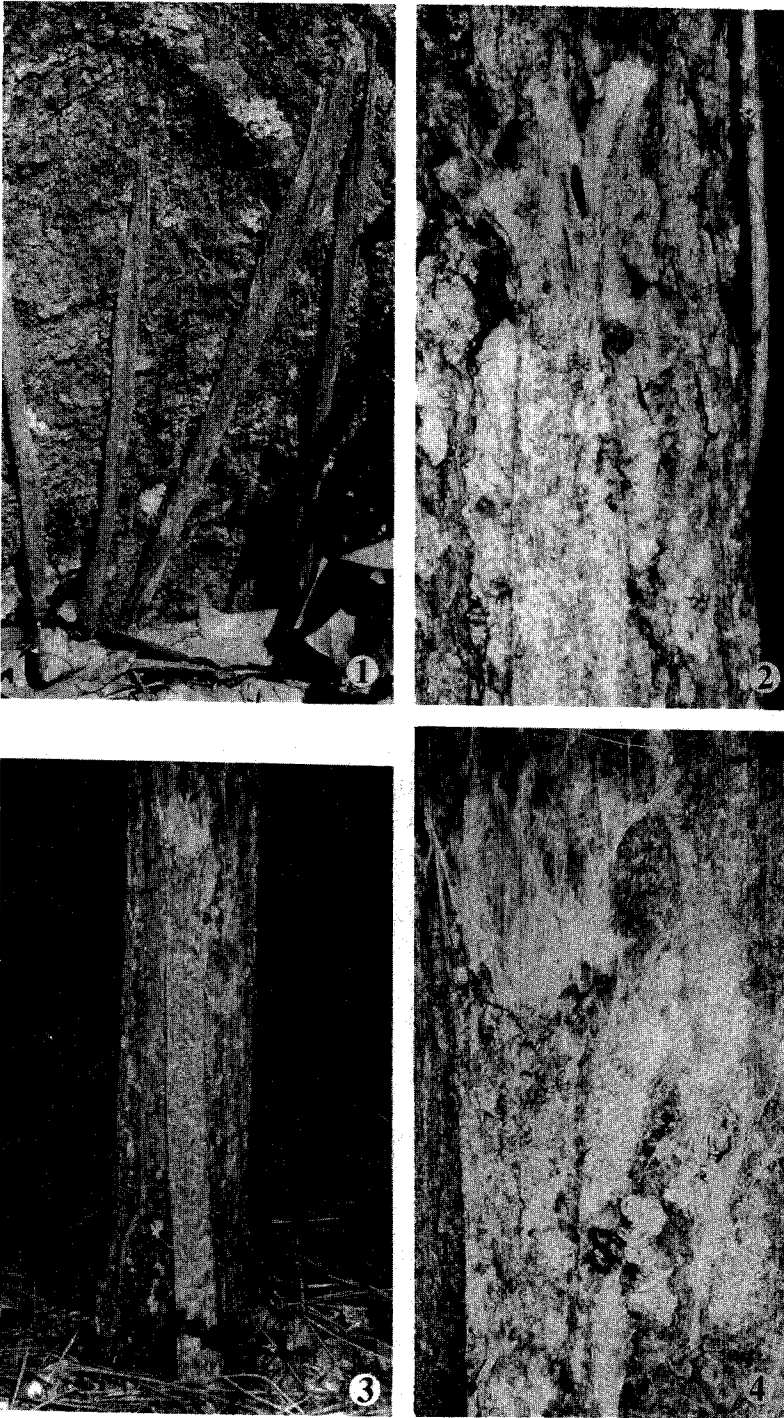
Habitat, microhabitat, and population density.—All three *S. abboti* populations were in the magnolia forest community of Shelford (1963). At Thomasville and Suwannee River the herbaceous ground cover was dominated by poison ivy (*Rhus*), Virginia creeper (*Parthenocissus*), ferns, and greenbrier (*Smilax*), whereas in the hammock community at Mud Springs, there was a dense cover of saw palmetto (*Serenoa*). At all localities the soil was a soft, grey, very sandy loam with much humus. The soil was humid but well drained, and was covered by a continuous layer of leaf litter. *S. abboti* tubes were absent from low stream bank areas subject to periodic flooding.

Population densities were high at all three localities, being on the order of several hundred tubes per hectare. Commonly, an occupied tree had more than one tube attached to it, and occasionally five or more tubes were attached to a single tree with only 0.5 to 4 cm separating some tubes (Fig. 1). At Thomasville, one 15-cm diameter post oak held one adult female tube and six other tubes nearly as large. Several larger trees held between twelve and fifteen tubes apiece. We observed, as did McCook (1888), that both adult and immature tubes were attached to a variety of hardwood tree species of all sizes, including saplings less than 4 cm in diameter. Because only a few of the pine trees examined supported tubes (pine trees were fairly common at Thomasville), it appears that hardwood tree trunks are more suitable microhabitats than pine trunks. Since the tubes are permanent constructions, added to over the life of the spider, it is likely that those spiders which attach tubes to pines might not be able to maintain them because of the tendency of the bark of most pines in the area to break off in large flakes, or plates.

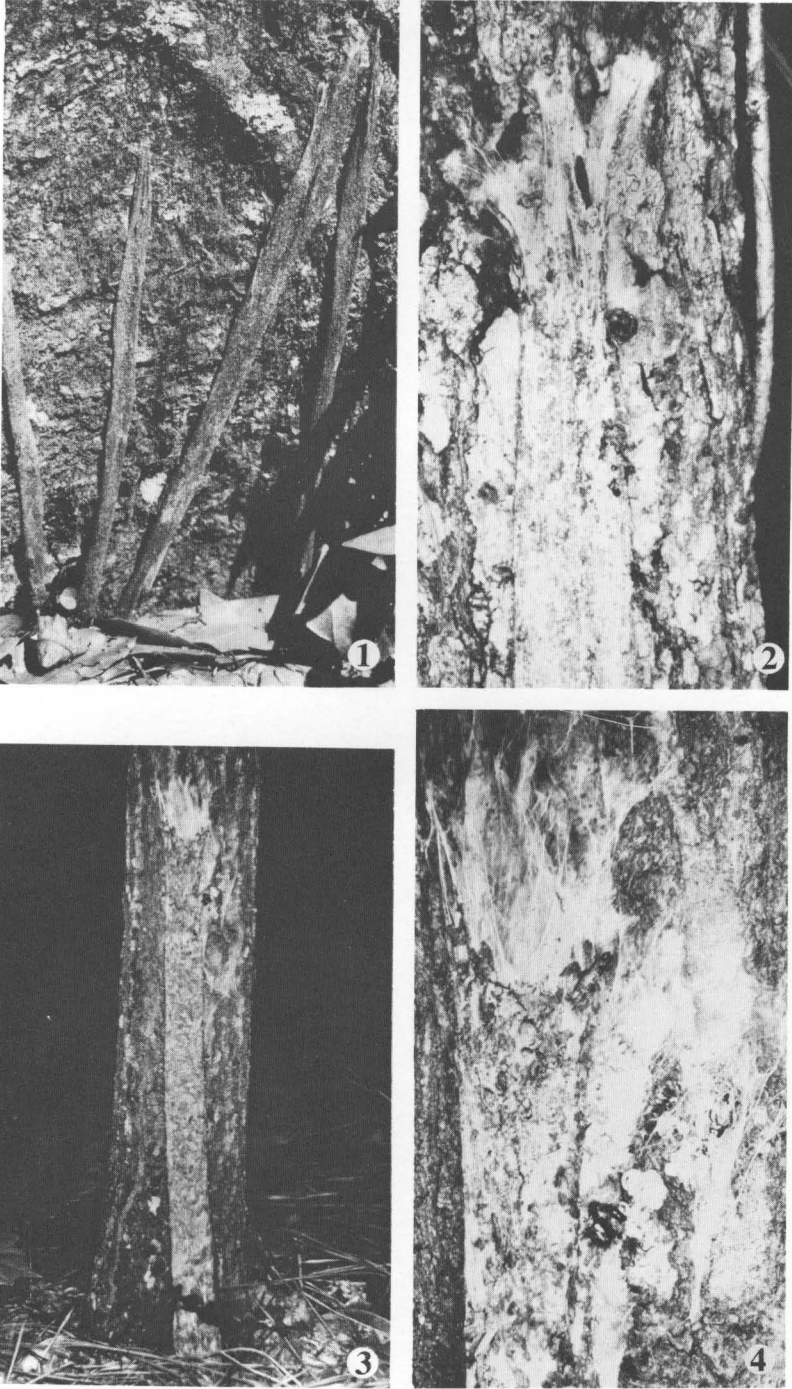
Phenology and spiderling development.—Our discovery at Thomasville on July 16 of two *S. abboti* males searching for females indicates, in accordance with the observations of Gertsch (1936) and Bishop (1950), that males emerge from their tubes and search for mates in July.

Evidently, egg sac construction and egg laying occur in August. This is indicated by the absence of egg sacs and spiderlings in all adult female tubes ($N = 15$) collected from Thomasville and Suwannee River on July 15, 16, and 19 and by the presence of second instar spiderlings in most of the adult female tubes collected at Suwannee River and Mud Springs on October 5 and 6.

An examination of six broods collected reveals much about the timing and pattern of postembryonic development in *S. abboti*. Five of the six broods consisted of second instar spiderlings. In the remaining brood of 89 from Suwannee River, 26 spiderlings were



Figs. 1-4.—Tubes of purse-web spiders: 1, four tubes of *Sphodros abbotti* on a large *Magnolia* trunk near Thomasville, Ga.; 2, upper end of a tube of *S. abbotti*; 3, tube of *Sphodros rufipes* on an unidentified hardwood tree at Florida Caverns State Park, Marianna, Fla.; 4, upper end of a tube of *S. rufipes*.



Figs. 1-4.—Tubes of purse-web spiders: 1, four tubes of *Sphodros abbotti* on a large *Magnolia* trunk near Thomasville, Ga.; 2, upper end of a tube of *S. abbotti*; 3, tube of *Sphodros rufipes* on an unidentified hardwood tree at Florida Caverns State Park, Marianna, Fla.; 4, upper end of a tube of *S. rufipes*.

very late in the second instar (third instar setae were visible beneath the outer cuticle), two were shedding the second instar cuticle, and 61 were in the third instar. One of the second instar broods from Suwannee River was kept alive at room temperature for 21 days and by the end of that period had developed to the third instar. These spiderlings were more heavily pigmented than the third instar spiderlings collected on October 6. The second instar (= first postembryonic stage of Yoshikura 1958) spiderlings are quite motile and possess well developed chelicerae and fangs, tarsal claw teeth, and numerous long setae, but they lack spines on the endites and have approximately ten spinneret spigots. Third instar spiderlings possess a more elongate body, many spines on the inner margin of the endites, and approximately 45 spinneret spigots. Yoshikura (1958) reported that the first instar (= Yoshikura's deutovum) of *Atypus karschi* (Donitz), which emerges from the embryonic cuticle and chorion at hatching and molts ten days later to the second instar, possesses stubby non-functional chelicerae and fangs, short tarsal claws without teeth, very short and widely scattered setae, and no spinneret spigots.

These data indicate that hatching in these populations of *S. abboti* occurs in September. Probably by late September the first instar spiderlings molt to second instar spiderlings, which then emerge from the egg sac. No egg sac remnants were found in any of the tubes containing spiderlings. The molt to the third instar takes place during October. These third instar spiderlings are anatomically equipped to handle prey and construct tubes, and, when placed on soil, they construct small silk tubes resembling the tubes of adults. Abbot's finding of a large number of spiderlings in their mother's burrow in November (McCook 1888) indicates that they overwinter there before dispersing in spring, but other authors (McCook 1888, Gertsch 1936, 1979) suggest that dispersal may occur in their first autumn.

Brood size.—The mean number of spiderlings in the six broods collected at Suwannee River and Mud Springs was 79.7 (range = 49-142, s. dev. = 35.98).

Tube architecture.—The tubes of 24 adult female *S. abboti* and of a smaller number of immature specimens were excavated, measured, and closely examined in the laboratory. As shown in Figs. 1, 2, and 5, these silk tubes consist of an underground portion which lines the burrow and an aerial portion which extends approximately straight up the tree trunk. The aerial portion of the tube is firmly attached to the bark and held taut by numerous silk attachment strands which are concentrated at its upper end (the upper 3 to 5 cm of the tube) and which often form broad apical attachment bands. Attachment strands are rare or absent below the upper one-third of the aerial part of the tube. This mode of tube attachment probably dampens prey-generated vibrations less than if the entire length of the tube were anchored to the trunk.

Contrary to the statements of Abbot (McCook 1888), McCook (1888), and Gertsch (1949) that the underground portion of the tube of *S. abboti* is as long or longer than the aerial portion, we found (Table 1) that the underground portion of the adult tube is usually well under one-half the length of the aerial portion. The aerial tube length/underground tube length averaged highest in the Thomasville population (mean = 3.4) and lowest in the Suwannee River population (mean = 2.3); the Mud Springs population was intermediate (mean = 2.7). The burrow, which is approximately circular in cross section, extends straight down into the ground, unless, as is often the case, roots cause it to turn towards the horizontal. Frequently the tube is enlarged just below the soil surface. Possible functions for this chamber are to house the egg sac (as in *Atypus affinis*, Eichwald [Enock 1885, Bristowe 1958]), to serve as a mating chamber, to allow more efficient prey handling during feeding, and to allow the spider to turn around more easily.

The bottom end of the burrow tapers and is occasionally two-branched or has one or two collapsed, apparently abandoned, branches.

Usually the aerial portion of the tube is nearly cylindrical close to the ground but becomes more flattened as it ascends the tree. A few tubes are nearly cylindrical throughout most of their length; others are more flattened than usual and have a collapsed look over much of their length. Because the tube is flatter near the upper end, its width (maximum diameter) remains approximately constant or increases slightly from ground surface to near the attachment zone, even though its circumference decreases slightly over the same distance. In the attachment zone the tube usually narrows considerably. A few tubes have collapsed side branches attached to the aerial portion. These apparently are tubes which were dislodged and have been replaced.

The entire inner surface of the tube is smooth white silk. The silk is thicker and the tube is consequently tougher underground than it is aboveground. Soil particles (mostly bits of humus) are embedded in the outer surface of the aerial portion of the tube. Frequently there is a partial covering of moss. As a result, the color of the emergent tube is primarily light to medium brown or greenish brown. Silk and soil particle density decrease with distance from the ground surface, so that the tube is darkest at its base and becomes lighter distally. In the attachment zone there is usually such a low density of soil particles in the tube that it is very light brown or white. Attachment strands are white.

In Comstock (1940) the claim is made that the tube is camouflaged by virtue of matching the bark to which it is attached and that this camouflage is the result of "minute bits of bark, lichens, and moss, which are evidently collected by the spider from the trunk of the tree and fastened to the surface of the web." Our observations of tube materials and tube construction behavior show that non-green materials in the tube are mainly soil particles excavated from the burrow and implanted into the tube from inside the tube (See also McCook 1888, and Gertsch 1979). Since the sand grains do not adhere to the silk as well as the lighter, flatter, and more irregular humus particles, the latter predominate.

The form and distribution of the moss on the tubes indicate that it is not transplanted by the spider but instead reaches the tube surface as spores. The moss grows in a thin layer on the tube surface and is not embedded in the silk. It usually decreases more rapidly in abundance with increasing distance from the base of the tube than does soil particle density. Only the protonema stage (often with buds) of the moss life cycle occurs on the upper (newer) part of the aerial portion of the tube.

Actually, by human visual standards *S. abbotti* tubes do not always match the adjacent trunk surface very closely in color. Because of this and their form, they look more like sticks or vines than a part of the bark surface. It appears likely to us that, in addition to reducing visual and tactile identification of the tube by potential predators and prey, the non-silk materials in the tube may also help to stiffen the tube wall and consequently help keep the tube expanded so that prey generated vibrations are not dampened and so that the spider's approach does not cause gross changes in the tube shape that could warn its prey.

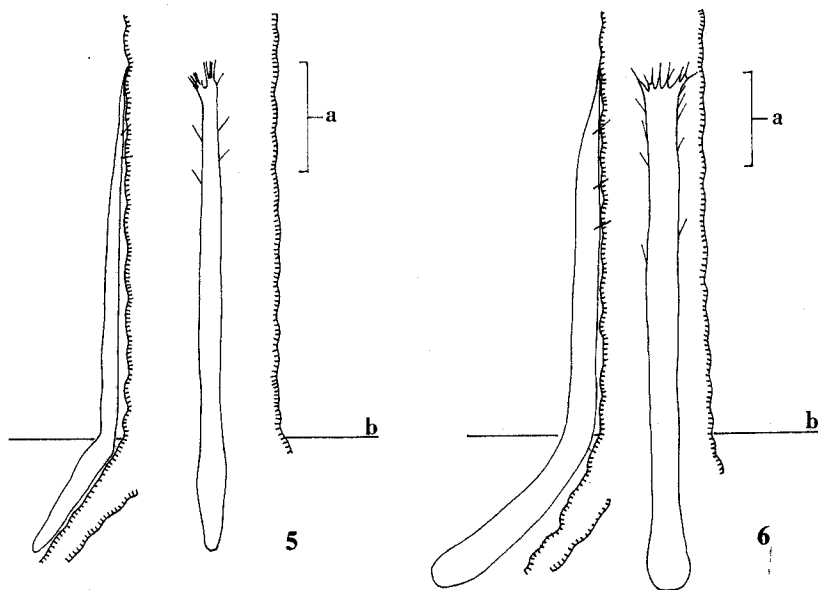
Trash Disposal.—Prey exoskeletons and *S. abbotti* molts are commonly found hanging loosely from the outside surface of the upper end of the tube. Since trash is rarely embedded in the tube silk and since trash is sometimes found on the ground near the base of the tube, it appears that the spider does not normally actively attach trash to the tube but that it simply lodges there as it is being pushed through the end of the tube. The thin exoskeletons of prey like spiders and crickets are finely fragmented and these fragments

are bound tightly together by silk into a compact ball. The harder exoskeletons of other prey (millipeds, beetles, isopods, etc.) are not so finely fragmented and these large pieces of exoskeleton are more loosely bound with silk. Molts are not fragmented and are bound with only a small amount of silk. No trash was found in the bottom end of any tubes.

Prey.—The following prey were identified from the trash attached near the tops of *S. abboti* tubes: 6 spiders (1 Clubionidae), 11 isopods, 6 millipeds (3 Julida, 3 Polydesmidae), 1 cricket, 11 beetles (3 Staphylinidae, 2 Carabidae, 1 Lampyridae, 1 Curculionidae), 7 worker ants, 1 wasp (*Vespula*) and 5 unidentifiable insects. One slug caterpillar (Limacodidae) had been killed but was discarded undigested. Evidently the primary prey of *S. abboti*, in the fashion of trapdoor spiders, are arthropods which frequent the ground surface, but unlike most trapdoor spiders, *S. abboti* captures some diurnal aerial insects like *Vespula*.

Reproductive Behavior.—Although courtship and mating behavior have been observed in some European *Atypus* (Enock 1885, 1892, Gerhardt 1929, 1933, Ehlers 1937, Bristowe 1958, Clark 1969), there is virtually no evidence for how males locate and recognize adult female tubes. There is no published data on reproductive behavior in American *Sphodros* species. Consequently, we were fortunate to observe two *S. abboti* males late in the afternoon of July 16 near Thomasville.

The first male was discovered inside the upper end of an adult female tube. As the tube was excavated, this male escaped through a slit in the top of the tube. The second male was spotted as it walked over the leaf litter near the base of the tree from which an adult female tube (the tube in which the above male was found) had just been removed. In behavior (rapid jerky movements), color (black with an iridescent purple abdomen), and form (relatively slender body and legs) the male resembled a large, black ant or a pompilid wasp. When it reached the tree trunk, it walked over its surface, and when it arrived at the position where the tube had been minutes before, it immediately turned



Figs. 5-6.—Diagrammatic composite drawings showing the major features of the tube of purse-web spiders: 5, *Sphodros abboti*; 6, *Sphodros rufipes*. a, zone of attachment; b, soil level. See text for further explanation.

and walked rapidly up the trunk in a straight path coincident with the natural position of the tube. It stopped abruptly where the upper end of that tube had been attached. It then pivoted back and forth as if searching for the tube. Then it walked down and laterally away from this point and stopped briefly on a medium sized tube, cut a slit in its upper end, but did not enter. It then moved around the trunk to another medium sized tube and examined it briefly before leaving it.

This male was then placed on the trunk of another tree about 15 cm from the undisturbed tube of an adult female. It walked around the trunk, stopped when it encountered this tube, turned, and walked up the tube to its top. It quickly cut a slit in the top with its fangs and immediately entered the tube. After hesitating in the top, it then descended rapidly. As the tube was excavated, the male returned to the top and escaped through the slit.

This male was later placed on yet another trunk near the spot where another adult female tube had been removed. It walked around the trunk, turned when it reached the position where the tube had been, walked up a path coincident with the tube's natural position, and stopped where its upper end had been. It then remained motionless for several minutes, was retrieved, and the observations were ended.

The evidence suggest that the diurnally wandering males of *S. abboti* have evolved a defensive mechanism of generalized wasp-ant mimicry in response to selection pressure from visual vertebrate predators. We speculate that diurnal mate searching, which does not seem to be the rule in burrowing mygalomorphs (Main 1957, Buchli 1962, Coyle 1971) and which is not the practice in some *Atypus* species (Bristowe [1958] calls the male of *Atypus affinis* "a night wanderer."), may increase the efficiency of tube finding for males of *S. abboti* by allowing visual orientation toward tree trunks, which can probably be perceived without large eyes. The nocturnal wandering of *A. affinis* males (Enock 1885, Bristowe 1958) is consistent with our hypothesis, since visual orientation toward *A. affinis* tubes, which are not attached to trees, would probably require a very sophisticated visual system.

The behavior we observed strongly suggests that adult female tubes of *S. abboti* are marked by a contact sex pheromone, some of which remains on the bark when a tube is removed. This is the first strong evidence supporting the hypothesis, hinted at by Bristowe (1958) but more completely developed by Platnick (1971), that the prime releaser of courtship and mating in *Sphodros* is a contact chemical produced by the adult female.

It is to be expected that immature spiders do not produce the pheromone. Then why did the male slit open one immature tube? There is at least one interpretation of this behavior which is consistent with the hypothesis that immature tubes lack the pheromone. Perhaps two stimuli, the sex pheromone and contact with a tube, are required to release the tube slitting response, so that contact with the immature tube, just a few seconds after stimulation by the pheromone of the removed adult female tube, completed the stimulus requirements for tube slitting. Enock (1885) observed that *A. affinis* males coming in contact with the tubes of mated females "immediately run away as fast as possible," without receiving an overt signal from the female. Bristowe (1958), however, felt that the ability of the *A. affinis* male to recognize the reproductive status of the female was based upon the presence or absence of an overt response by her to his drumming on the tube with palpi and legs, a male pattern which we did not see. Bristowe says that "if the female is immature or pregnant his advances from the outside of the tube are repulsed by another signal—a sharp tug or series of tugs at the tube" Obviously there is a need for careful study of *Sphodros* and *Atypus* courtship behavior.

Table 1.—Tube dimensions for adult female *Sphodros* spiders.

	<i>S. abboti</i> (N=24)			<i>S. rufipes</i> (N=4)	
	Range	Mean	Std. dev.	Range	Mean
Total length (cm)	24-45	31.1	4.82	33-52	41.5
Length of aerial portion (cm)	18-35	22.8	4.11	18-35	25.8
Length of underground portion (cm)	5-13	8.6	1.78	14-17	15.8
Aerial length/underground length	1.6-5.4	2.8	0.77	1.2-2.1	1.7
Tube width (max. diam.) 1/3 of its length above ground (mm)	10-20	16.2	1.73	18-24	21.5

SPHODROS RUFIPES

Habitat, microhabitat, and population density.—At both Florida Caverns and Torreya, *S. rufipes* is found in mixed hardwood forests (the beech-magnolia forest of Braun [1950]) which share a number of constituents with the mixed hardwood forests of the Southern Appalachians. The Torreya forest is dryer, more open, and has a much sparser ground cover than the forest at Florida Caverns. The soil at both localities is very sandy loam, but is dryer at Torreya.

In both populations of *S. rufipes* tubes were found on a variety of hardwood trees species, but there appeared to be a decided preference for small trees, a relationship which Muma (1944) also observed. At both localities, in spite of the presence of many larger trees, tubes were found only on trees with diameters from 2-45 cm (mean = 10.4 cm s. dev. = 5.17, n = 10) with all but three of these trees being under 8 cm in diameter. However, as Gertsch (1979) and Jackson et al. (1978) have observed, *S. rufipes* tubes are sometimes attached to large trees.

At Florida Caverns and at Torreya, the *S. rufipes* tubes were widely scattered, with population densities of less than 50 tubes per acre. Only two trees were found supporting more than a single tube. Each of these trees supported two tubes. Similar densities were reported for the Maryland populations of *S. rufipes* studied by Muma and Muma (1945). Thus the demography of *S. rufipes* appears to be very different from that of *S. abboti*.

Tube Architecture.—The following description is based upon close examination of excavated tubes of four adult female and six immature *S. rufipes* specimens. Adult females of *S. rufipes*, which are much larger than *S. abboti* adult females, construct wider tubes with a proportionately shorter aerial portion (Figs. 3, 4, and 6; Table 1) The numerous attachment strands of the attachment zone (the upper 3-6 cm of the tube) flare out and form a white sheet often a bit wider than the tube. Below the attachment zone are no more than three attachment points. The tube is flattened near the top and becomes more rounded as it descends to the ground surface. The width (maximum diameter) of the aerial portion is nearly constant throughout its length. Muma (1944) and Muma and Muma (1945) report markedly longer underground tubes for Maryland *S. rufipes* than we observed in Florida. Perhaps this difference results from harsher soil environments in Maryland. Underground the *S. rufipes* tube bends slightly to strongly

toward the horizontal. It is slightly constricted immediately below the soil surface but is enlarged near the bottom end to harbor the egg sac (Muma and Muma 1945) or to serve other functions.

The silk is thickest at and below the soil surface, and becomes thinner and more fragile as the tube ascends the tree. Below the mostly white attachment zone, the aerial tube varies from light grey-brown or greenish grey-brown to darker brown or greenish brown, the upper part being lighter than the lower part. As in *S. abboti* tubes, most of the non-silk material consists of excavated organic soil particles which, because of their greater surface area and lighter density, probably adhere better to the silk than do the sand grains. Two tubes were poorly camouflaged with only a sparse covering of soil material in the upper one-half of their aerial portions. Usually moss is also present on the tube surface, but its form and distribution, as on *S. abboti* tubes, indicate that it is not transplanted by the spider. Old shriveled aerial tubes lay in the litter attached at the ground surface to two of the adult female tubes.

Trash Disposal.—As in *S. abboti*, large amounts of prey rejectamenta and parts of two molts were found loosely attached to the upper end of *S. rufipes* tubes. The exoskeletons of soft-bodied prey are macerated into tiny fragments which are then bound together with silk into a tightly packed ball, whereas hard prey exoskeletons are broken into fewer, larger, more loosely bound fragments. The only trash found in the bottom ends of tubes were parts of one molt and pieces of a male *S. rufipes* exoskeleton.

Prey.—The following prey items were identified in the trash collected from *S. rufipes* tubes: 4 spiders (3 *S. rufipes* males), 2 isopods, 6 millipeds, 2 crickets, 17 beetles (4 Cerambycidae, 1 Carabidae, 1 Scarabaeidae), 1 ichneumonid wasp, 4 worker ants (1 *Camponotus*), 1 caterpillar, and 5 unidentifiable insects. It appears from this and from the data of Muma and Muma (1945) that the diet of *S. rufipes*, like that of *S. abboti*, consists mainly of a great variety of ground surface arthropods.

Reproductive Behavior.—Collection data accompanying four *S. rufipes* male specimens we have observed from North Carolina, Tennessee, and Maryland indicate that they search for mates in June and are diurnal, like *S. abboti*. It would be interesting to witness the behavior of the brightly colored *S. rufipes* males (red legs; black body, chelicerae, and pedipalps) to see whether mimicry or warning coloration might be involved. The macerated exoskeletons of three *S. rufipes* males found with the tubes of the two adult *S. rufipes* females indicate that they sometimes fall prey to their (intended?) mates.

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