

POST-HATCHING DEVELOPMENT AND WEB PRODUCTION OF *HYPTIOTES CAVATUS* (HENTZ) (ARANEAE, ULOBORIDAE)

Brent D. Opell

Department of Biology, Virginia Polytechnic Institute and
State University, Blacksburg, Virginia 24061

ABSTRACT

Members of *Hyptiotes cavatus* construct vertical triangle-webs, consisting of only four radii spanned by capture threads. Spiderlings began constructing triangle capture webs only as third instars. In the laboratory male and female development was synchronous, most individuals maturing as sixth instars, at which time males ceased constructing capture webs. Capture webs were usually constructed only during the first sixty percent of a developmental stadium. Males and females reared in large containers produced more webs during and spent more time in the fifth stadium than those reared in small containers with more closely spaced supports. Development and web production of earlier instars were not significantly influenced by container size.

INTRODUCTION

Hyptiotes cavatus (Hentz) are common in the eastern half of the United States (Muma and Gertsch 1964) where their webs are often found in the lower branches of conifers. This relatively stable habitat affords a large number of web attachment points and seems to support a relatively constant population throughout the spring and summer. These spiders produce vertical triangle-webs which have only four radii with cribellar capture "spirals" extending between them (Fig. 1; Comstock 1913, Emerton 1902, Gertsch 1979, McCook 1884, Wilder 1875). Webs of this type are also produced by *H. flavidus* (Blackwall) (Castelnau and Thorell 1897), *H. gertschi* Chamberlin and Ivie (Muma and Gertsch 1964; personal observations), and *H. paradoxus* (C. L. Koch) (Marples and Marples 1937, Peters 1938, Wiehle 1927) and are probably characteristic of the genus' six other species. This web form is thought to be a reduced and reoriented horizontal orb-web, the primitive and most common web form of the family Uloboridae to which *Hyptiotes* belongs (Opell 1979).

Associated with web reduction and change in orientation is a more active mode of web monitoring and use during prey capture. Rather than hanging beneath a horizontal web's hub as the family's orb-weaving members do, *Hyptiotes* hold their webs taut while resting near the attachment of the apex line (Fig. 1). Here their robust body form renders them inconspicuously bump-like. When a prey contacts the web the spider releases about a centimeter of slack silk held by the fourth legs, causing the web to be shaken, apparently to ensure prey entanglement and perhaps to allow evaluation of prey weight. After one or

several web jerks the spider runs down the apex line (often collapsing the web) and wraps the prey, initially by throwing silk over it and eventually by more complete wrapping as the prey is rotated while being held with the second and third legs. In the process of capturing even a small prey the web is often completely destroyed, eaten by the spider, and usually replaced the following night. This is in contrast with orb-weaving uloborids which often repair their webs before replacing them (Eberhard 1972; personal observations).

The life cycle of *H. cavatus* also contrasts with that of the eastern temperate orb-weaving species, *Uloborus glomosus* (Walckenaer). The former matures in late August and early September and females produce attached, plano-convex eggsacs, each containing five to 12 eggs, which pass the winter and from which spiderlings emerge early the following spring (Kaston 1948, Scheffer 1905, Wilder 1875; personal observations). Members of *U. glomosus* mature in June and early July and produce suspended, stellate eggsacs, each containing 30 - 60 eggs (Kaston 1948; personal observations). Spiderlings emerge from these eggsacs later the same summer and overwinter as immatures.

Many questions about the biology of *H. cavatus* remain unanswered. The purpose of this study is to investigate the species' post-hatching development and web construction. Specifically, this study will determine: 1) the number and duration of post-hatching stadia, 2) how many webs are produced during each stadium, 3) what portion of each stadium is devoted to prey capture, and 4) what effect sex and available support spacing have upon these factors. This quantitative information about the species' development should be useful in designing future ethological and ecological studies of this intriguing species.

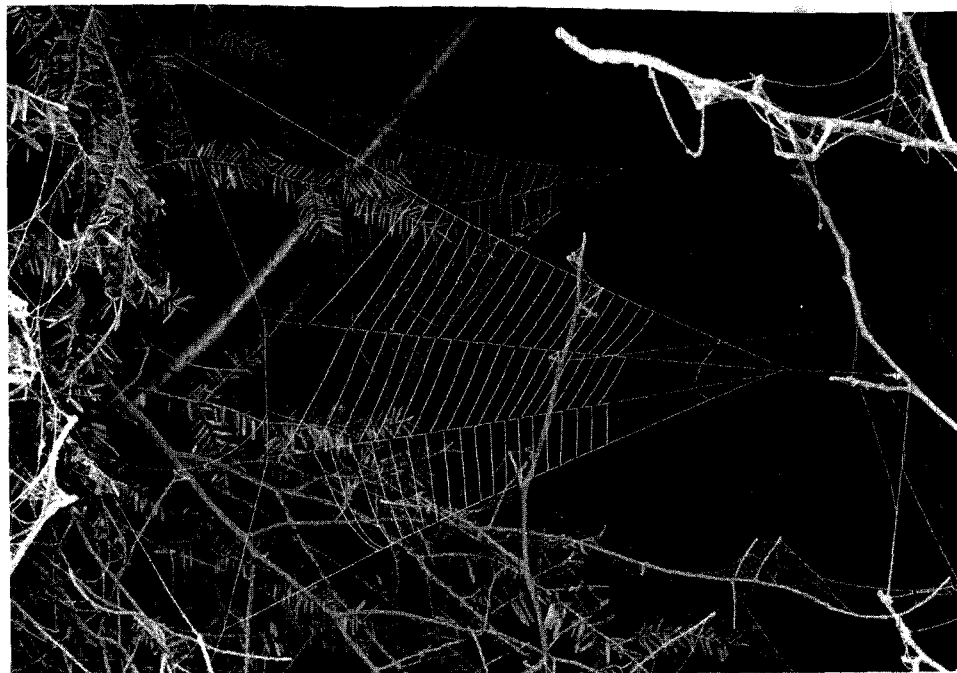


Fig. 1.—Webs of *Hyptiotes cavatus* adult female (foreground) and fifth instar male (background), 0.78 natural size.

METHODS AND MATERIALS

Laboratory observations were conducted on spiders reared from eggsacs collected on 25 November 1978 from the lower limbs of a single hemlock (*Tsuga canadensis*) near Newport, Giles County, Virginia. Eggsacs were refrigerated and, as spiders were needed, incubated at 23 to 25°C. Individuals were reared in separate plastic containers measuring either 30 x 16 x 8.5 cm or 34.5 x 25.5 x 16.5 cm. Wooden dowel rods cemented into larger containers formed a 30 x 23.5 cm rectangle at the container's center. Those cemented into smaller containers formed polygons of various sizes, the smallest being a 14.5 x 13 x 6.5 cm triangle and the largest a 26.5 x 15.5 cm rectangle. All containers were kept in a chamber where conditions of 23 to 25°C, 85 to 95% relative humidity, and a 10:14 hour light:dark cycle were maintained.

Laboratory studies were conducted from 14 January to 1 July 1979, during which time a total of eight males and 13 females were reared either to maturity (17 specimens) or to the penultimate instar, at which time the individual's sex could be determined. Spiders were observed daily except for eight instances involving an average of seven specimens in which one day was missed, three instances involving an average of four specimens in which two days were missed, and one instance involving three specimens in which three days were missed. The feeding regime consisted of blowing one wild type *Drosophila melanogaster* into each web produced. Exuvia and alcohol preserved adults were placed in individual vials and carapace and femur measurements later taken at 50x with a micrometer-equipped dissecting microscope.

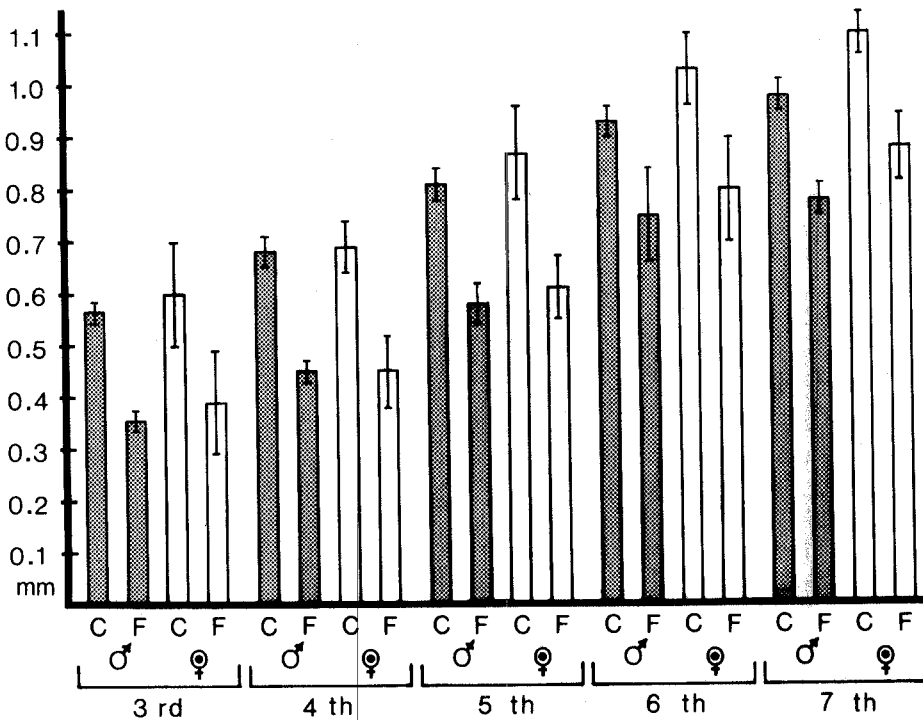


Fig. 2.—Changes in carapace (C) and fourth femur (F) lengths during development of male and female *Hyptiotes cavatus*.

RESULTS

Overview of Development.—*Hyptiotes cavatus* eggsacs are small, dark brown to gray, oval, plano-convex objects that are tightly appressed to the small lower branches of conifers (Scheffer 1905). Each of 11 field-produced eggsacs opened contained seven to 12 ($\bar{X} = 10$) 1 mm-diameter eggs. Spiderlings hatched and molted once within the eggsac before making a single, small exit hole in the eggsac's convex surface. Like other uloborids, newly emerged second instars lacked a functional cribellum and calamistrum (structures used to make cribellar prey-capture silk which is stretched across the web's four radii) and they hung for three to six days in an adult-like posture from short horizontal or diagonal threads until they molted a second time. Possessing a functional cribellum and calamistrum, these third instars constructed capture webs typical of the species. Adult male *H. cavatus* lacked a functional cribellum and calamistrum and did not construct capture webs. Males lived from 16 to 24 days after reaching maturity.

Third instar spiderlings constructed webs in the small container's smallest polygons and appeared to have difficulty producing webs in the large container. For this reason, most spiderlings were transferred to large containers only after they became fourth instars. Third instars successfully subdued, wrapped, and fed upon the same strain of *D. melanogaster* given subsequent instars.

Two males and two females matured as seventh instars and had longer carapaces and fourth femora than the remaining six males and 11 females which matured as sixth instars (Fig. 2). This is similar to Berland's (1914) findings that *Uloborus plumipes* Lucas matured in five molts. Within a given stadium abdominal enlargement was evident and similar in males and females. After molting, these gains were negated and the abdomen assumed the same proportionally slender appearance seen early in the previous stadium. Carapace and femur lengths of females usually exceeded those of males in the same stadia (Fig. 2), but T-tests showed these differences to be significant ($p < 0.05$) only for sixth instar carapace length.

Duration of Stadia.—The duration of each stadium and the proportion of this time during which webs were constructed are given in Figure 3 and the number of webs produced in Table 1. Webs were not constructed during the latter 35-50% of each developmental stadium. This period (REST) was subtracted from the length of each stadium (DURATION) to determine the number of potential feeding days (WEB-CONSTRUCTION). DURATION represents total time devoted to a developmental stage, WEB-CONSTRUCTION; the time spent acquiring energy and material necessary for growth; and REST, the final phase of development signifying either that enough resources have been obtained and/or that a phase has been entered in which prey capture activities are either not possible or would interfere with developmental events.

The independent and crossed effects of container size and sex upon DURATION, WEB-CONSTRUCTION, and REST in the third, fourth, and fifth stadia and upon the total days spent in each period were tested using Analysis of Variance tests (ANOVA). The only parameters significantly influenced ($p < 0.05$) were DURATION and WEB-CONSTRUCTION periods of the fifth stadium, both of which were affected by container size. In small containers males spent an average of 16.0 days in the fifth stadium, 10.7 of those being feeding days. Female values were 17.1 and 11.1, respectively. In large containers values for males were 18.0 and 12.0, respectively and those for females 21.5 and 16.2, respectively.

There were no significant differences between the DURATION, WEB-CONSTRUCTION, and REST periods of the third, fourth, and fifth stadia, as tested with ANOVA.

Number of Webs.—Independent and crossed effects of container size and sex upon the number of webs produced during third, fourth, and fifth stadia and upon the total number of webs produced during these three developmental stadia were tested with ANOVA. Of these parameters, only instar significantly influenced ($p < 0.05$) the number of webs produced. The greatest number of webs were produced during the fifth stadium and the least during the fourth stadium (Table 1).

DISCUSSION

Overwintering by *Hyptiotes cavatus* differs from that of *H. paradoxus*. During the summer, populations of the latter species are comprised both of individuals which have emerged from eggsacs early in the spring and half-grown individuals which emerged late the previous summer and passed the winter as immatures (Wiehle 1927). In *H. cavatus*

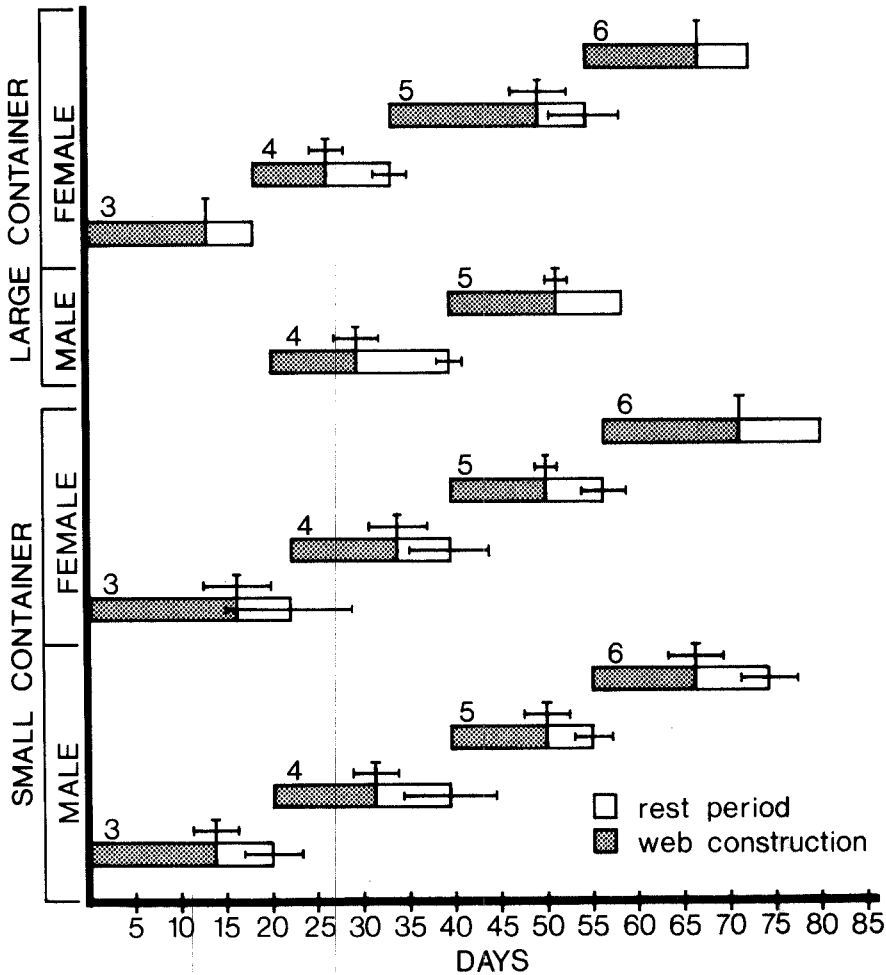


Fig. 3.—Developmental periods of *Hyptiotes cavatus* third, fourth, fifth, and sixth instar males and females reared in small and large containers. Intervals at the right of boxes represent sd of stadia and those above sd of web construction periods.

Table 1.—Web production during *Hyptiotes cavatus* development [\bar{X} and (sd)]

INSTAR	SMALL CONT.		LARGE CONT.		BOTH CONTAINERS		
	male	female	male	female	male	female	all
Third	4.6(2.2)	4.7(2.3)	—	4.0	4.6(2.2)	4.6(2.2)	4.6(2.1)
Fourth	3.5(1.1)	3.3(0.7)	2.0	3.7(1.2)	3.1(1.1)	3.4(0.8)	3.3(0.9)
Fifth	4.7(1.4)	4.9(1.6)	5.5(0.7)	5.5(1.4)	4.9(1.3)	5.2(1.5)	5.1(1.4)
TOTAL	13.3(3.4)	13.4(3.1)	—	14.0	13.3(3.5)	13.5(2.8)	13.5(3.0)
SAMPLE SIZE	6	7	2	6	8	13	21

only third instar individuals and webs were seen in the spring of the two consecutive years. Likewise, adults were seen only in late summer. This discrepancy may represent a population rather than a species difference, but published accounts of *H. cavatus* reproduction and life history are not specific enough to resolve the question.

Unlike members of several orb-weaving uloborid genera (Eberhard 1969, 1977, Opell 1979, Peters 1953, Szlep 1961, Wiehle 1927), second instar *Hyptiotes* did not construct a non-cribellar horizontal mesh web for prey capture. Instead, they hung from resting threads for several days until they molted again and were able to construct triangle-webs. Inactivity of second instars is similar to that reported for *Miagrammopes* species (Lubin et al. 1978), but is of longer duration. Because the primitive uloborid genera (Opell 1979) *Tangaroa* and *Waitkera* construct orb-webs (J. A. Beatty, personal communication, Forster 1967), the orb-web must be considered plesiomorphic for the Uloboridae and the webs of *Hyptiotes* and *Miagrammopes* apomorphic. Structural and behavioral specializations associated with construction of these two reduced (specialized) web forms may preclude production of a non-cribellar capture web similar to that made by young orb-weavers and favor a short, non-feeding second stadium.

Third instar spiderlings were collected in the field as early as 7 July and adults as early as 23 August, indicating that mean laboratory developmental times of 55-60 days (for spiders which mature in the sixth stadium) were close to field development times. Because lab-reared specimens were fed only a small prey item each time they made a web and because prey capture usually resulted in web destruction, laboratory results may overestimate the number of webs normally produced. However, if spiders normally capture less than one prey per day these results more nearly reflect field averages.

Under the laboratory feeding regime male and female development was synchronous. DURATION, WEB-CONSTRUCTION, and REST periods of third and fourth stadia were statistically constant in large and small containers. However, in the fifth stadium spiders reared in large containers had longer DURATIONS and WEB-CONSTRUCTION periods. As nearly all web and wrapping silk was reingested by the spiders, this effect was probably due to the greater amount of energy required to produce larger webs found in large containers. This explanation is supported by a higher mean number of webs produced by fifth instars of both sexes reared in large containers (Table I). Since lab-reared spiders were fed one fly per web and very few webs were destroyed while being measured (most damaged webs were third instar webs), the number of webs is a good index of energy requirements during fourth and fifth stadia. As shown by time spent feeding on *Drosophila* and by dry weights of discarded prey, fourth, and fifth, and sixth instars extract a fairly constant amount of material from each prey (Opell, in preparation). This indicates that in order to construct their webs in large containers fifth instar females

required additional energy roughly equivalent to that derived from 0.6 *Drosophila*. This is in general agreement with Peakall and Witt's (1976) finding that silk formation and web construction require relatively little energy.

Ethological and ecological contrasts between *H. cavatus* and other uloborids as well as orb-weavers of other families make this species an excellent subject for future study. The rearing procedures, developmental observations, and influence of support spacing upon development presented in this study should facilitate such studies.

ACKNOWLEDGMENTS

I thank Robin M. Andrews for making comments on an earlier version of this manuscript.

LITERATURE CITED

- Berland, J. 1914. Note sur le cycle vital d'une Araignée cribellate, *Uloborus plumipes* Lucus. Arch. Zool. Expér., 54 N R:45-57.
- Castelnau, J. and T. Thorell. 1897. Notes sur *Hyptiotes anceps*. Feuille J. Nat., (3)27:107-111.
- Comstock, J. H. 1913. The Spider Book. Garden City, New York: Doubleday, Page, and Co.
- Eberhard, W. G. 1969. The spider *Uloborus diversus* Marx (Uloboridae) and its web. Ph.D. Thesis, Harvard University, Cambridge, Massachusetts.
- Eberhard, W. G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). J. Zool. London, 166:417-465.
- Eberhard, W. G. 1977. The webs of newly emerged *Uloborus diversus* and of the male *Uloborus* sp. (Araneae, Uloboridae). J. Arachnol., 4:201-206.
- Emerton, J. H. 1902. The Common Spiders of the United States. Boston: Ginn and Co.
- Forster, R. R. 1967. The spiders of New Zealand (part 1). Otago Mus. Bull., 3:1-184.
- Gertsch, W. J. 1979. American Spiders, 2nd ed. New York: Van Nostrand Reinhold Co.
- Kaston, B. J. 1948. Spiders of Connecticut. Conn. Geol. Nat. Hist. Surv. Bull., 70:1-874.
- Lubin, Y. D., W. G. Eberhard, G. G. Montgomery. 1978. Webs of *Miagrammopes* (Araneae: Uloboridae) in the Neotropics. Psyche, 85(1):1-23.
- McCook, H. C. 1894. American Spiders and their Spinning-work. Vol. 3. Philadelphia, pp. 1-285.
- Marples, M. J. and B. J. Marples. 1937. Notes on the spiders *Hyptiotes paradoxus* and *Cyclosa conica*. Proc. Zool. Soc. London (A), 107:213-221.
- Muma, M. H. and W. J. Gertsch. 1964. The spider family Uloboridae in North America north of Mexico. Amer. Mus. Novitates, 2196:1-43.
- Opell, B. D. 1979. Revision of the Genera and Tropical American Species of the Spider Family Uloboridae. Bull. Museum Comparative Zoology, 148(10):443-549.
- Peakall, D. B. and P. N. Witt. 1976. The energy budget of an orb web-building spider. Comp. Biochem. Physiol., 54 A (2):187-190.
- Peters, H. M. 1938. Über das Netz der Dreieckspinne, *Hyptiotes paradoxus*. Zool. Anz. 121(3-4):49-59.
- Peters, H. M. 1953. Beiträge zur vergleichenden Ethologie und Ökologie tropischer Webspinnen. Zeits. Morph. Ökol. Tiere, 42:278-306.
- Scheffer, T. H. 1905. The cocooning habits of spiders. Kansas Univ. Sci. Bull., 3(2):85-114.
- Szlep, R. 1961. Developmental changes in web-spinning instinct of Uloboridae: construction of the primary-type web. Behaviour, 27:60-70.
- Wiehle, H. 1927. Beiträge zur Kenntnis des Radnetzbaues der Epeiriden, Tetragnathiden und Uloboriden. Zeits. Morph. Ökol. Tiere, 8(3-4):468-537.
- Wilder, B. G. 1875. The Triangle Spider. Pop. Sci. Monthly, 1875(April):1-15.