The Orb Web during the Life of *Argiope aurantia* (Lucas)

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REED, CHARLES F. (1969). *The Orb Web during the Life of Argiope aurantia (Lucas).* DEVELOPMENTAL PSYCHOBIOLOGY, 2(2): 120–129. Changes in size, quantity, and regularity of detail were followed in the orb webs of *Argiope aurantia* Lucas for 8 laboratory-born females reared under controlled environmental conditions. Mesh width and the number of radii decreased steadily from the 3rd month of life to death. Thread length and area of web reached peaks around the time of the last molt and sexual maturation, and decreased thereafter. Leg length, weight, and molt, while related to web characteristics, do not account entirely for changes in dimensions. Furthermore, after several months under similarly controlled conditions, 6 females that had been caught outdoors built unusually large webs. The characteristic changes of *Argiope aurantia* webs in the laboratory appear to reflect not only physiological maturation and decline, but may be related to early experience with the efficiency of the web as a trap.

garden spider orb-web invertebrate innate behavior maturation early experience field *vs* laboratory data

WHILE ITS GENERAL form remains constant, the orb web of *Argiope aurantia* Lucas (Levi, 1968) changes in size and in number of thread elements throughout the life span of the animal. Some of these changes appear to be linear and therefore related to dimensions of the spider's body and perhaps to the output of silk; others show single peak periods probably attributable to maturation of the spider. Superimposed upon these events is a considerable daily variation that is not eliminated by controlling feeding, temperature, light, humidity, and accessibility to physical structures upon which the webs are built.

Our purpose in this paper is to describe the development of webs of *Argiope aurantia* in the laboratory and to attempt to relate it to bodily growth (measured in body weight and leg length), and to the webs of other species of orb-weavers (Wiehle, 1927; Tilquin, 1942; Witt & Baum, 1960). In attempting to supplement these data, captured spiders were placed under laboratory conditions after the main collection of data was underway. Some differences that emerge between the two samples have challenged assumptions we have made previously regarding the relevance of the early history of the spider.

In the laboratory, *Argiope aurantia* (Fig. 1) molts five to seven times between hatching and death (12 to 18 months after hatching). There is a close correlation between body weight and length of leg until the final molt, when the spider is sexually mature and the abdomen of the female swells with eggs. The relationship then becomes less clear, but there is presumably still a complex interaction of organ systems. Another uncertain period occurs in younger spiders

Received for publication 20 June 1969.

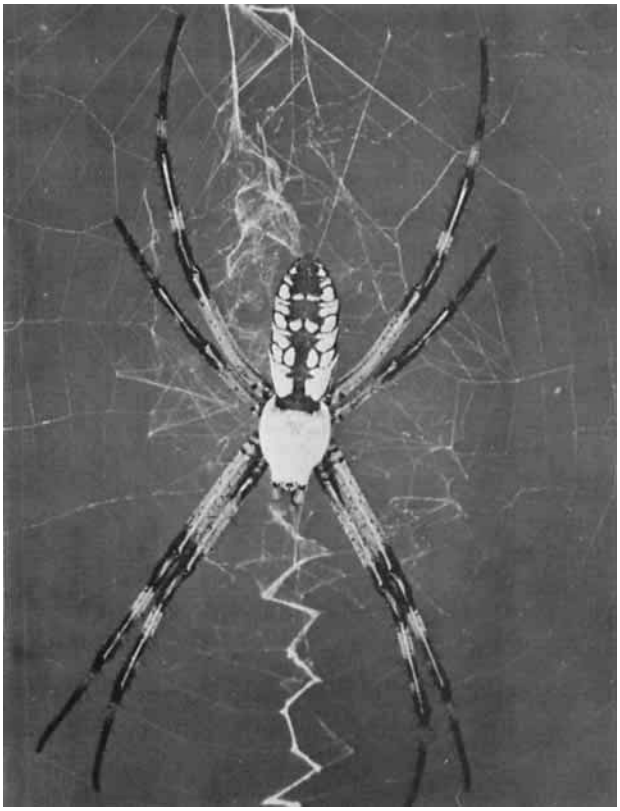


FIG. 1. This inverted position is taken at the center of the web by the adult female *Argiope aurantia* Lucas as it waits for prey.

during molting. Webs built then are small and have relatively few threads. At molt, apart from the effort of sloughing the old exoskeleton, neural and sensory systems are in complex transitional states.

The web of *Argiope aurantia* is shown in Figure 2. It is built in the laboratory essentially in a vertical plane and consists of dry radii supporting the viscid spiral thread. A hub or platform is separated from the spirals by a free zone. The hub of the web may or may not include a stabilimentum: a thick band of threads placed over the hub of the web at the very end of construction (appearing as a broad white structure in the center of Fig. 2). It is not certain that this structure has a function; none has been identified (*see* Discussion). In fact, there is no orderly pattern of appearance or growth of the stabilimentum throughout the lifetime of a laboratory-reared spider, as far as we have been able to determine from examination of successive webs of individual spiders.

Webs are built fairly regularly on a daily basis, although there may be periods of several days between webs. The movements in building webs are considerably slower than those of *Araneus diadematus,* a comparatively short-legged species of orb weavers.

METHOD

Eight female spiders were selected from a group that hatched in mid-January in the laboratory; they emerged from a single cocoon found outdoors. The cocoon had been placed in a box filled with gnats, and the spiderlings could build webs and catch prey freely. The first molts were observed on January 27 and the first webs on January 29.

At the beginning of March, the animals were moved to 12 × 16 cm wooden frames, which were in turn placed in 50 × 50 × 8 cm aluminum and glass cages. Light was turned on at 8:00 a.m. and off at midnight. Onset of light was accompanied by a steep rise in temperature. Humidity was kept at a constant high level. Each animal received 5 houseflies (*Musca domestica*) and 5 drops of water per week during this period.

At the end of March, the wooden frames were removed from the cages, and web-building in the glass and screen cages was recorded daily. All spiders continued on the same feeding regime and were weighed about every 3 weeks. Mean weight gain for all animals is shown in Figure 3; individual growth curves differed considerably; on the same day in May one spider weighed 108 mg while its equally healthy litter mate weighed 18.7 mg. We were unable to obtain any reduction in this variability. The 8 spiders upon which we report were selected because of their high production of webs and the full record thereby provided. Of the 43 original hatchlings, only 22 were females; 9 had died by June 1, 12 by the middle of July, 14 by November.

For purposes of evaluation of webs, the cage doors were removed every morning, the animal removed from the web, and the threads sprayed with Krylon white enamel (development of photographic technique ultimately enabled us to obtain webs suitable for measuring without spraying). Photographs were taken on high contrast copy film with the web placed against a deep black background with fluorescent illumination from 4 sides.

Points of thread intersection and attachment were measured in the manner described by Witt *et al.* (1968). A computer program extracted a variety of expressions of web geometry and dimensions from these raw measures; in general, they dealt with size, regularity, and shape of the structure. Size measures are the total length of thread composing the web and the areas of the principal regions of the web. Figure 4 diagrams these regions; the roughly ring-shaped catching or spiral area is surrounded by the open spaces of the frame and scaffolding and encloses the center area where the spider awaits prey. Regularity refers to the spacing of threads between the spirals (4 cardinal

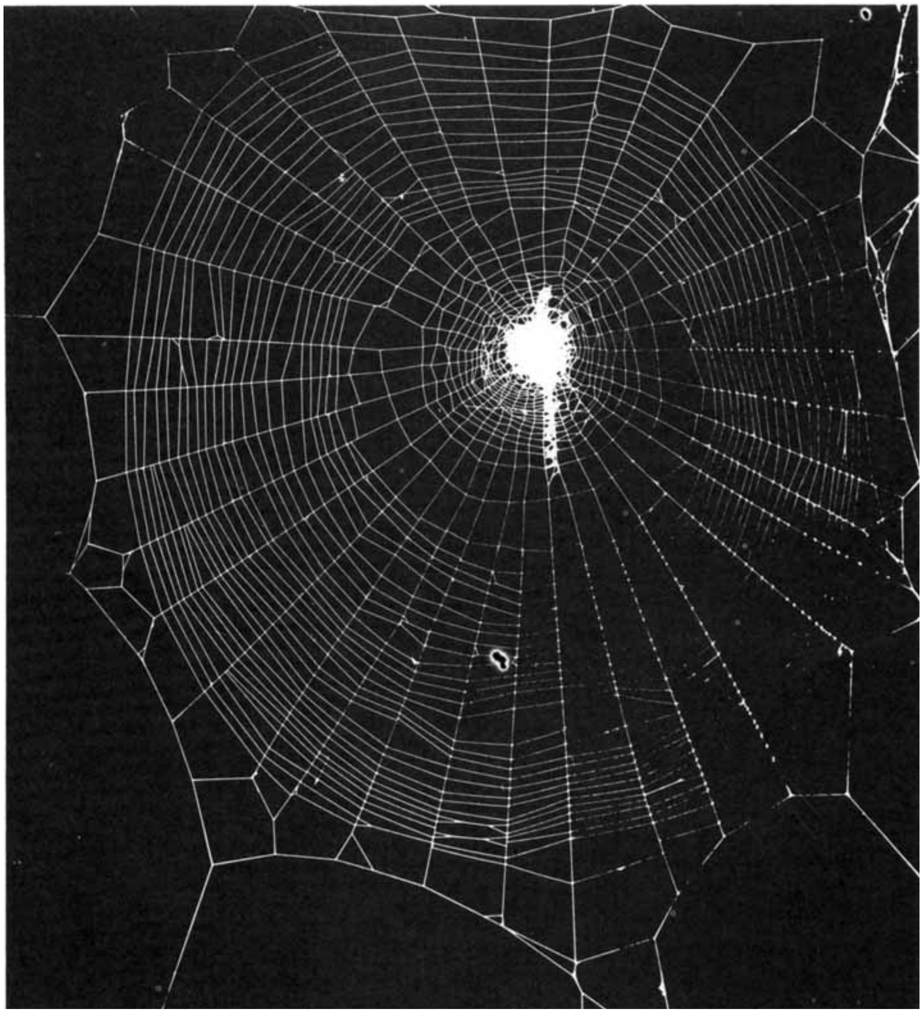


FIG. 2. Web of adult female *Argiope aurantia* of captured group, built in October. All available data indicate that this spider was about the same age as the spider that built the web in Fig. 5(*b*). Characteristically for the whole group, this web is larger and was built with more radii and spiral turns, but has a similar mesh width to the web in 5(*b*). The weights of the animals were 177 and 192 mg, respectively, and can hardly explain the difference in webs.

directions were measured), and to the equality of central angles between radial threads. Shape of the web is indicated by deviation from a circular form and asymmetry of the hub with respect to the spiral zone. Finally, thread density in the catching zone, a web-index that does not fall into any of the 3 categories, is calculated by dividing the area of the catching zone by the product of spiral turns and radial number. This index, mesh size, assumes that the catching zone is subdivided into compartments of equal size (which it is not); it provides an expression of the expenditure of thread used to subdivide space. A large catching zone with many threads and a small catching zone with few threads can yield identical mesh sizes.

In addition to data for spiders that spent all of their lives in the laboratory from cocoon to death, we have obtained web measures for 6 female *Argiope aurantia* caught outdoors at the end of July and beginning of August. Their weights in mid-August corresponded to the April weights of the laboratory-reared group; we have concluded from this and other evidence (date of last molt, death date) that they hatched about 4 months later than the laboratory animals (i.e., at the usual date for wild *Argiope aurantia* in the Raleigh, N. C., area).

After the captured spiders were brought into the laboratory, both groups spent their lives in identical cages with identical feeding and environmental control.

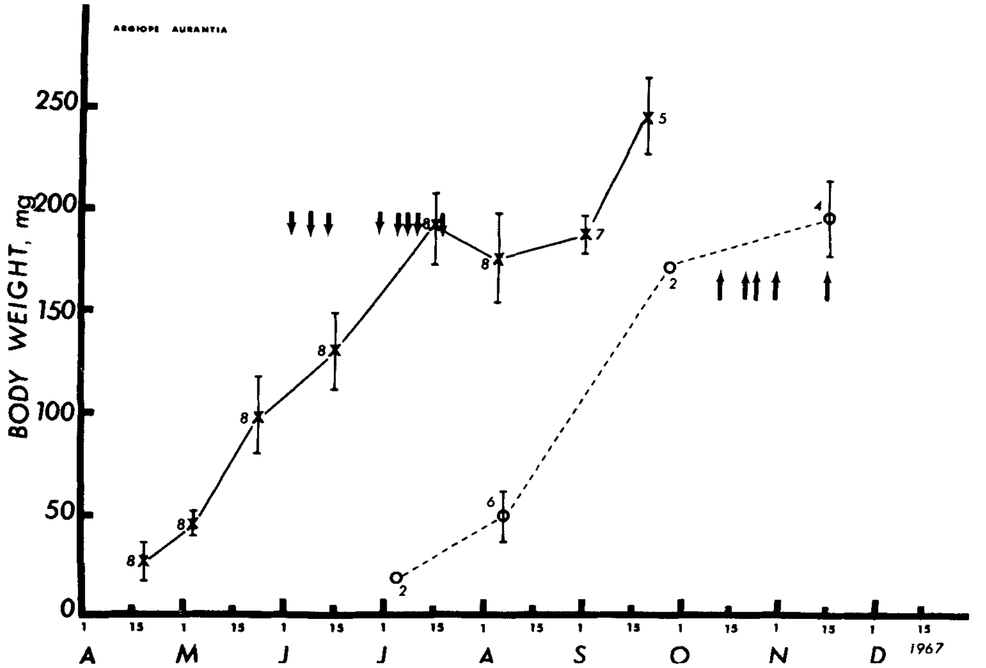


FIG. 3. Mean weights (crosses) and standard errors (lines) of female *Argiope aurantia* littermates between April 19 and September 25. The mean length of forelegs of the same group in May-June was 20.25 ± 0.3 mm. Open circles indicate mean of the few weights obtained for 6 female *Argiope aurantia* caught outside; their mean leg length in October 1967 was 23.40 ± 2.0 mm. Arrows pointing down show dates on which spiders of the first group molted, arrows pointing up indicate molting-dates for second group.

If one assumes that the unknown hatching date of the second group was about 4 months later than that of the first group, body measures show, in contrast to web measures, no noticable difference between the 2 groups at comparable ages.

RESULTS

LABORATORY HATCHLINGS

The findings are summarized in Figures 3 to 9. As Figure 3 indicates, body weight of the laboratory-born animals increased in an essentially linear manner until the passing of the last molt. Although not recorded on the figure, leg length would show saltatory rather than continuous growth. Length of the first leg actually was measured on the molted limb.

It may be noted parenthetically that the chart shows a similar course for the spiders captured out-of-doors, although measurements were taken less frequently than for the laboratory spiders. The 2 curves appear to be parallel, but displaced in time by about 4 months.

WEB-DIMENSIONS

In the figures that follow, data for all laboratory animals are combined for each period. This procedure seemed justified by the approximately equal levels of building activity. All webs are included in the graphs, including those built directly before and after molting. We assumed that the mean accurately represents the individual, that is, that we are dealing with a single set of similar curves. The wide variation between consecutive webs for single spiders makes it very difficult to check that assumption.

Characteristic webs at 3 life stages for the same spider are shown in Figure 5.

SIZE AND DENSITY

The most orderly course of development occurs in the most abstract index, mesh size. Figure 6 shows an essentially linear growth in mesh size throughout the lifetime of the sample. Moreover, in contrast to most other measures, the variation in mesh size is small. The course of growth is parallel for the laboratory-hatchlings and for the captured animals. Since this measure is an expression of the relative density of threads in the catching zone of the web, it appears that as the animal ages the web network assumes a relatively more open character.

One element in the computation of the mesh size is the number of radii composing the scaffolding of the web. Figure 7 indicates a steady decline in number of radii for *Argiope aurantia,* progressively fewer radii being constructed as the animals age. Tilquin (1942)

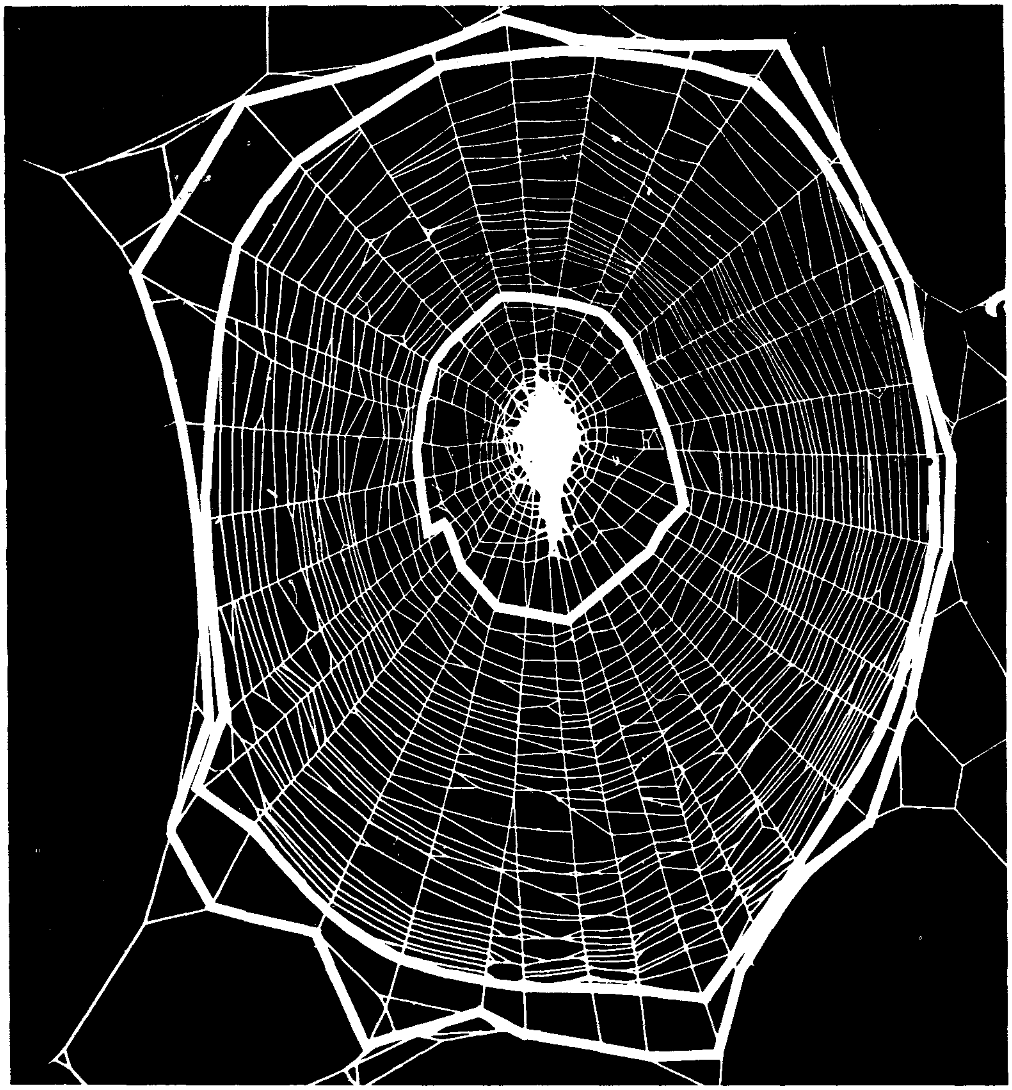
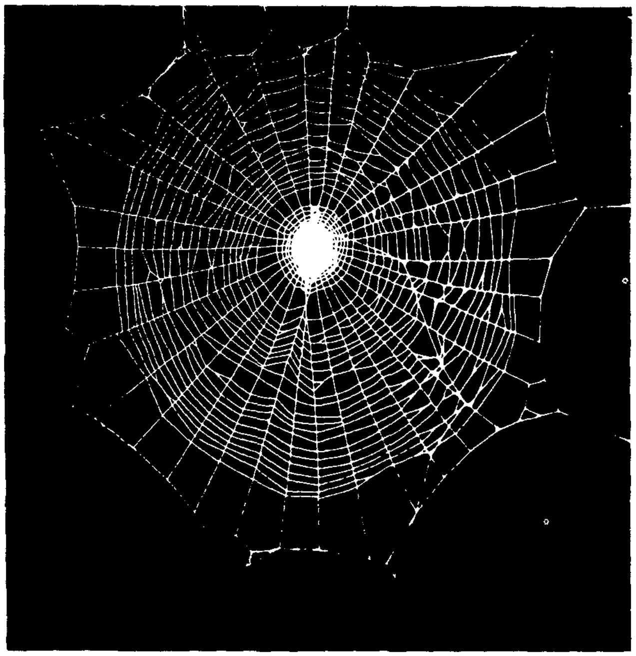


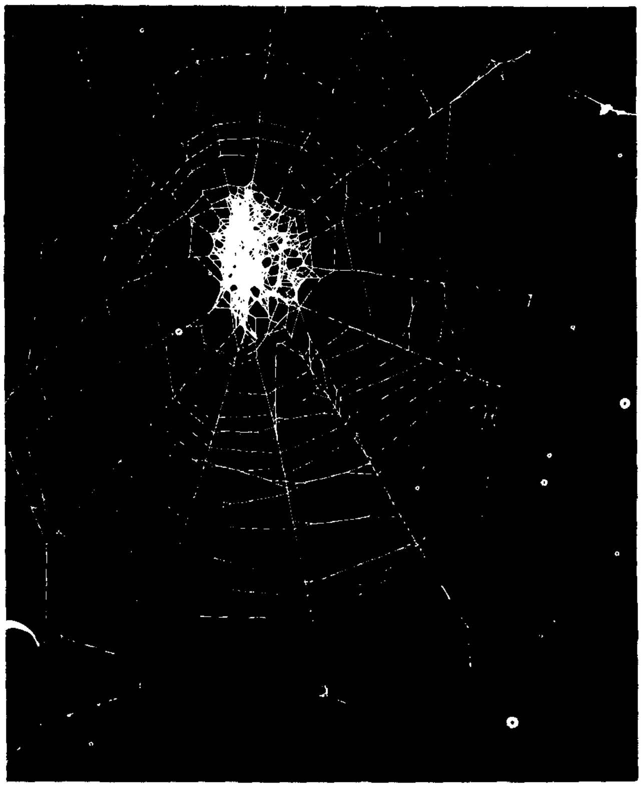
FIG. 4. Photograph of web of adult, laboratory-reared female *Argiope aurantia*. The thick white lines surround the central area, spiral or catching zone, and frame zone. Note that the outermost line does not follow the framing threads exactly; this simplification is for computational convenience.

found a relatively small number of radii in the very first and early webs of *Argiope aurantia* (Page 31, Table 3). Our graphs do not include such early webs. Wiehle (1927) counted higher numbers of radii in the webs of young *Araneus diadematus* than in those built by old animals. The second expression in the denominator in the formula for mesh size is the number of spiral turns in the catching zone. These measures taken separately for the upper and lower part of the web (not illustrated) range uncertainly in the early stages of growth, but show a clear decline after July; a parallel decline occurs for the captured spiders in November. On the other hand, the numerator in computation of mesh size, the area covered by spiral zone (Fig. 8), shows growth and decline. The peak magnitude for the area of the catching zone is reached in the July measures for the laboratory hatchlings and in November for the captured animals.

There is thus a kind of reciprocal relationship between the three expressions that compose the mesh size measure (area of the zone, number of radii, number of spiral turns), such that their combined net effect is to produce a steady reduction in thread density. Unfortunately, this expression is a statistical abstraction of uncertain biological significance. It represents a computed space measure; a quadrilateral space that would represent an optimal distribution of threads in the space composing the catching zone. The actual meshes of the web (the spaces bounded by 2 adjacent radii and 2 adjacent spiral turns) vary systematically



A



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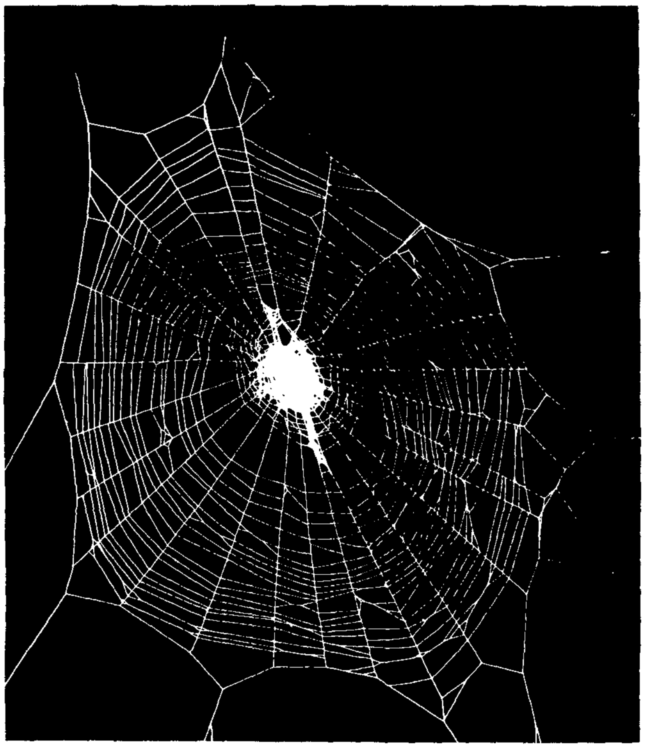

B

FIG. 5. Three webs built by the same spider (laboratory group). Webs are shown to scale and were built (*a*) in April, body weight 25 mg, leg length 10 mm; (*b*) in July, body weight 180 mg, leg length 23 mm; and (*c*) in October, body weight 250 mg, leg length still 23 mm. Note characteristic changes in web size and detail during 7 months of observation. *See* Figs. 6 to 9.

from central to peripheral regions of the zone and unsystematically according to the regularity of placement of radial and spiral threads (*see* Fig. 2).

It cannot be inferred simply that the mesh size matches the capacity of the spider to span space with its legs, or that it is appropriate to the size of the prey with which the spider is capable of coping. For the present, we may merely note that the density of thread elements in the web of *Argiope aurantia* diminishes throughout the lifetime of the animal.

Figure 9 shows that thread length, the total linear measure of thread used in all parts of the web, diminishes during the later part of life. Thread expenditure reaches a peak in July for the laboratory hatchlings and 4 months later for the captives. Perhaps a more precise statement would be that the path the spider takes in building becomes shorter. We have good reason to believe, but have not proved for this species, that with increasing weight of the builder the thread becomes thicker. An old spider's web, with relatively short total thread length, could contain as much material as a web with a relatively long total thread length built by a lighter (younger) spider (Christiansen *et al.*, 1962).

The first innermost turn of the sticky spiral marks the outer boundary of a zone called the center area.

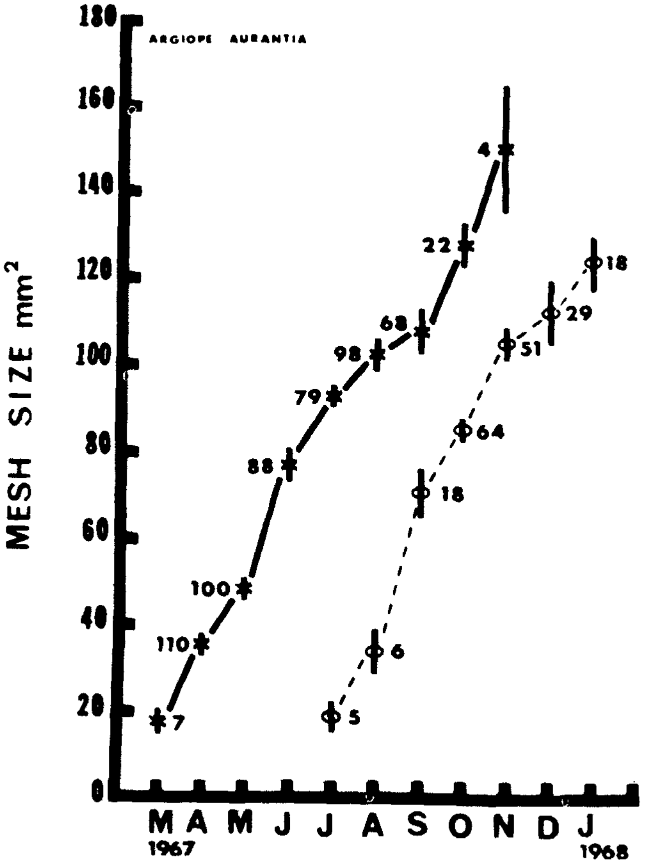

FIG. 6. Mesh width (total area of catching zone divided by number of radii and number of spiral turns) increased evenly throughout lifetime of both groups.

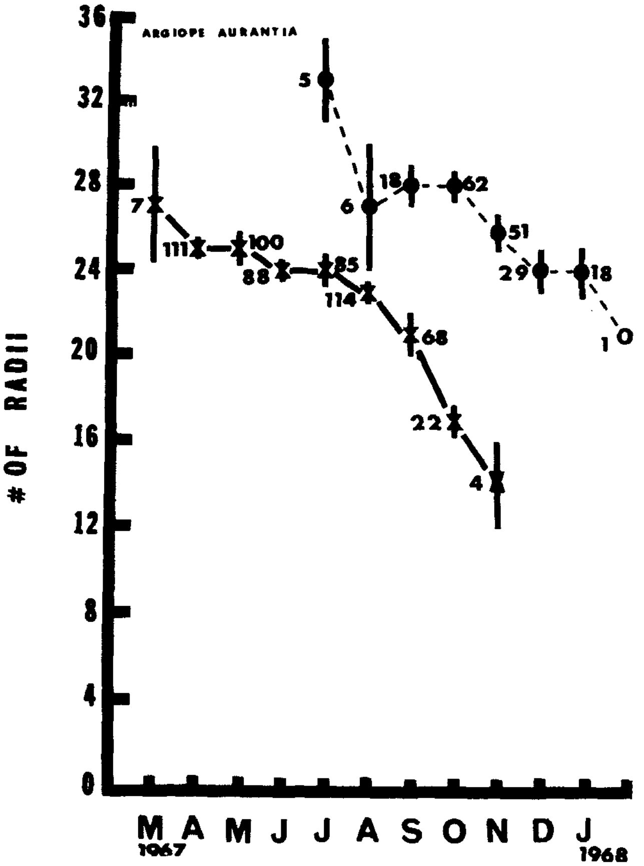

FIG. 7. Number of radii, showing decrease throughout observation period indicated on abscissa. Webs of the captured group always showed a larger number than did webs of the laboratory hatchlings.

It includes the hub and free zone. Peters (1937) has described for *Araneus diadematus* what is in effect a positive correlation between leg length and size of center area. By contrast, our *Argiope* data show a peak curve for the center area, similar to that of the spiral area.

REGULARITY

The foregoing data are concerned with thread output and area of the web. But the web is also characterized by a certain degree of precision of placement of threads. Adjacent central angles differ little from each other, the variation of differences is affected by certain kinds of treatment; for example, removal of 2 ipsilateral front legs severely affects central angle regularity (Reed *et al.*, 1965). The comparative irregularity of central angle in the older spider could be an artifact of our computation, which is contaminated by the relatively larger central angles. The measure for spacing of spiral turns is, however, relatively precise and stable. As shown by an index of relative spiral deviation, the regularity of this spacing progressively declines throughout the spider's life (early webs: $\overline{X}=0.46$ mm; late webs: $\overline{X}=0.70$ mm).

SHAPE AND SPECIAL CHARACTERISTICS

Finally, the overall shape of the web seems to remain constant; a slightly oval web with hub in the upper portion remains characteristic.

We have not been able to verify the impression that young spiders build stabilimenta more frequently (Comstock, 1948, p. 204) or more elaborately (Levi, 1968, p. 338) than the adult. The stabilimentum was not given up in captivity, as Wiehle (1927) found for *Argiope bruennichi.*

The stabilimenta may differ in role and development for species that build them. Definition of the structure differs with each author. We include the portion of thread overlaying the hub; other writers may refer only to the bands extending into the free zone. Whatever the definition, however, the structure is highly variable in form throughout the development

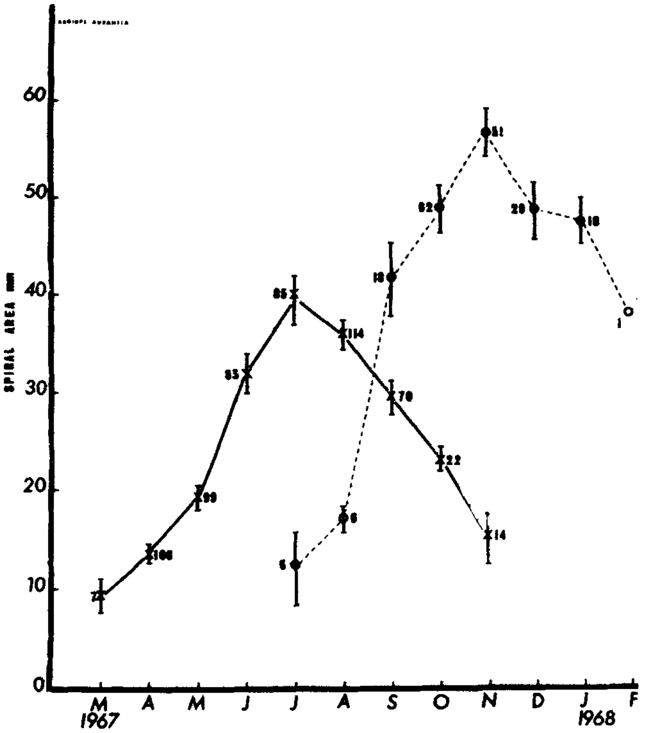

FIG. 8. Spiral area means are plotted for all webs built in each month; vertical lines indicate standard errors. Note, however, that data for the active period were available for only 8 spiders. The small figures indicate number of webs in each group. Note that peak size of zone coincides roughly to time of last molt and sexual maturation in each group, and is significantly higher for the wild group, even though they had been in the laboratory for more than 4 months.

of *Argiope aurantia;* there is no obvious pattern or change in complexity.

This variability fails to support any of the functions hypothesized for the stabilimentum: that it stabilizes or strengthens the web, conceals or camouflages the spider, acts as guide or clue for the male's location of the female (Crome & Crome, 1961). In the absence of a contemporary function, it may be possible, as has been conjectured by Gertsch (1949, pp. 180–181), that construction of the stabilimentum is a vestige of once functional behavior.

A COMPARISON OF BUILDING SEQUENCES

Witt and Baum (1960) have reported web development characteristics for *Araneus diadematus* Cl. and *Neoscona vertebrata* McCook. Both species showed linear functions for body growth (weight and leg length) and an accompanying linear function for mesh area. Neither species appears to demonstrate the peaking effect for spiral area that occurs for *Argiope aurantia* Lucas. The number of radial threads at stages of development may distinguish the 3 species (very early *Argiope* webs were not recorded). Number of radii for *Argiope* shows a steady decline, *Neoscona* retains a relatively constant number, and *Araneus* reaches a plateau after a rapid but negatively accelerated rise in the first 2 months.

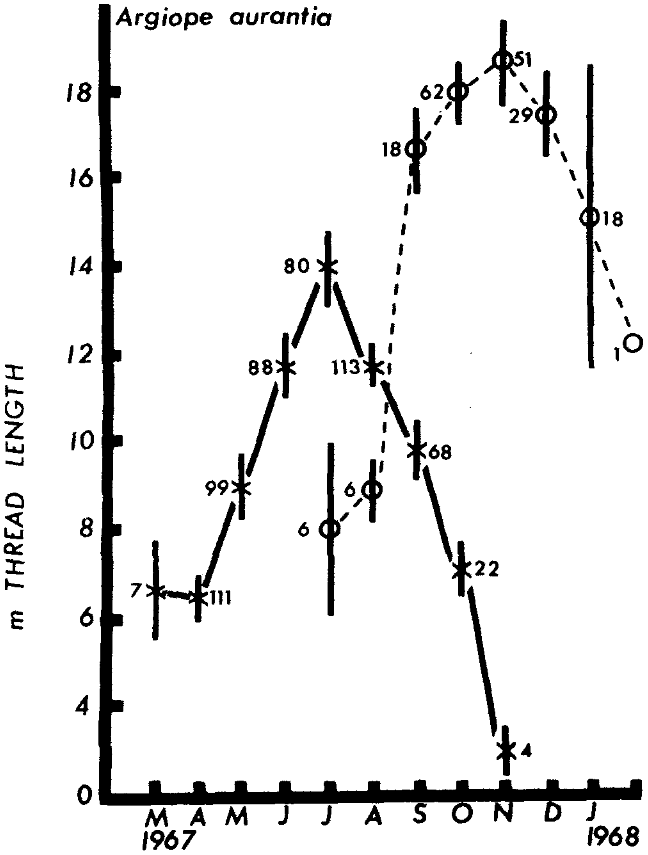

FIG. 9. Thread length during growth of wild and laboratory-reared *Argiope aurantia.* Vertical lines indicate standard error of means. Note parallel increase and decrease in curve, with significantly higher values at peak for captured spiders, following peak of laboratory group by about 4 months.

CAPTIVES AND LABORATORY HATCHLINGS: DEVELOPMENT AND MODIFICATION OF BUILDING-BEHAVIOR

Although the developmental curves for the laboratory hatchlings resemble those of the captives, some differences are apparent.

Several indices of web size show roughly parallel courses for the 2 groups of animals, but with peak levels that are significantly higher for the captives than for the controls. Figures 7, 8, and 9 contain the findings for radial number, spiral area, and total thread length, respectively. These measures are relatively independent, but conjointly indicate a high level of activity and expenditure of thread. It is important to note that development is parallel until the peak period. This early similarity makes it less likely that selection has eliminated those wild spiders that might have built small webs.

DISCUSSION

We have supposed that web dimensions depend upon the spider's bodily dimensions. The relationship is obviously complex. The addition of weights to the cephalothorax of *Araneus diadematus* has been shown to reduce size and number of thread-elements in the web (Christiansen *et al.,* 1962). Moreover, young *Araneus* with relatively long legs and light bodies build large webs with narrow meshes (Witt *et al.,* pp. 48–50).

For our spider there was a positive association between leg length and length of thread only up to the peak period; long-legged animals covered more space than short-legged animals. The captured group included the three spiders with the longest legs and one with the shortest legs of all animals in the study. The last animal produced webs with greatest mean thread length. Statistical tests fail to show significant differences, but the small number of animals involved would require considerable difference for significance to be reached.

Nevertheless it appears that, contrary to our surmise, web size cannot simply be explained by length of the spider's leg. Other hypotheses for the difference in web characteristics seem to be required.

If body dimensions are not sufficient predictors of web dimensions, what factors might account for the observed differences? Environmental physical constraints were the same for laboratory and wild spiders, and both groups of spiders had lived in the laboratory for several months. Several possibilities exist. Seasonal factors may have overridden the uniformity of laboratory conditions. Alternatively, the first four months in the wild may have initiated conditions that became evident only at maturity in the captured spiders.

With respect to the first possibility, it is true that the captured animals hatched and grew to maturity at the time of year characteristic for their species, whereas the laboratory-reared animals were, in effect, forced into early hatching.

The possible effect of an early existence in the wild is difficult to identify. It might be imagined, however, that the demands for expenditure of thread in nature are greater than in the laboratory, and that rate of growth for glands was set by depletion rates occurring early in the animal's life. There is no evidence at hand to support this speculation, and it is not clear how to use it to account for the decline in thread expenditure that occurs in the later half of the life of *Argiope aurantia.*

There is some evidence that feeding experience in the web affects production of new webs. Spiders never permitted to catch prey and to feed in the web, but supplied with flies and water in the same quantities as web-feeders, produced significantly fewer webs than did those allowed to remain and feed in the webs they had built. More particularly, each of the latter built a new web daily during an 11-day observation period, whereas none of the other group built every day (Chi square significance $<.01$). (Webs were always destroyed after feeding). The reduction does not appear to result from exhaustion of the web material.

Related modifications in behavior have been reported by Bays (1962) and by LeGuelte (1969), who attempted to train orb-weavers to particular cues. LeGuelte found that *Zygiella-x-notata* took progressively less time to return to its retreat in repeated trials following rotation of the web to an uncharacteristic position. Young animals or those that had been allowed to build only a few webs learned the new route more rapidly than old, web-experienced spiders.

Bays (1962) paired tuning forks of two different frequencies with palatable and unpalatable booty placed in the web, and found that the two tones could be discriminated. Moreover, a new discrimination followed reversal of the pairing of cue and booty, and the learning showed retention over several weeks.

Modification of attack and retreat behaviors apparently is possible for orb-weavers. Modification of the program of web-building is rather more difficult to demonstrate. In the first place, there are structural requirements that cannot be drastically altered. The web itself is an apparatus for reducing the variability of the spider's environment. That is, the spider's nervous system equips it to deal only with a small number of contingencies; the demands for learning are few. However, even in the favorably-biased environment of the web, there are emergencies and an occasional need for adaptation (e.g., in catching a potentially dangerous insect, in repairing damaged portions of the web). LeGuelte and Bays worked within this limited repertory of behaviors. The web is a product of a different form of adaptation than is represented by learning.

Nevertheless, it is possible that the differences in the webs of captive and laboratory hatched spiders may be due to learned behaviors rather than to the glandular factors mentioned previously. As usual, maturation must be distinguished from learning. Peters (1969), for example, has shown that *Zygiellae* removed from the cocoon earlier than the normal time for emergence produce incomplete and irregular webs.

The general question of the possible effects of experience upon the later history of web construction is presently under investigation in this laboratory. We have in the past assumed, in analogy to computer operations, that the web is the product of an innate program that was concurrently modified by input data regarding environmental and bodily conditions (mooring, weight, thread supply). A possibility that must now be entertained is that the central program is susceptible to another kind of alteration required by the data with which the animal deals early in its life. Those data could set rates of development for maturation and capacity of organs in the fashion already hypothesized for the silk glands. On the other hand, there may be a form of reinforcement of behavior by the catching of prey that followed web-building. We have presented some observations suggesting that frequency of building can be affected by the feeding procedures; perhaps web dimensions are also subject to these variables.

NOTES

Supported by National Science Foundation Grant Number GB-6246X1 to Peter N. Witt.

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