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Ontogeny of Web-building Behavior in Two Orb-weaving Spiders

PETER N. WITT

Research Division, North Carolina Department of Mental Health, Raleigh, North Carolina 27611

JOHN O. RAWLINGS

Department of Statistics, North Carolina State University, Raleigh, North Carolina 27607

AND

CHARLES F. REED

Department of Psychology, Temple University, Philadelphia, Pennsylvania 19122

SYNOPSIS. Spiders of similar mass but of two different species, *Araneus diadematus* Cl. and *Argiope aurantia* L., build webs which have similar geometric patterns, but which differ in relative proportions and thread number. Within species, webs may also differ reliably, presumably on a genetic basis. Fine detail of the web undergoes change throughout the lifetime of the spider, different for male and female; these changes are not simply responses to the growing weight of the spider. Relatively simple restraints, such as availability of material for thread, result in adaptations of web-building which may at first appear to be based upon building experience, but which are in fact independent of it.

It is possible to conceive of the form of the orb web as the necessary outcome of the physical restrictions imposed upon a thread-placing apparatus (the spider). The threads must support a spider of a certain mass, endure violent movement, and remain a functional snare for many hours. It would be expected that webs of the same class, e.g., vertical cartwheel orbs, would resemble each other in form.

At the same time, it would be expected that there would be variations in the web set by physical dimensions of the spider, e.g., weight. Beyond the physical demands for placing a thread network, there would be functions particular to the developmental stage, sex, or species of the spider – all somehow innately programmed into execution of web-building.

The cartwheel webs of different species may resemble each other because of the engineering requirements of structure and thread, or because of similarity of central nervous system programming. There are particular features such as the stabilimentum of *Argiope* and the open sector of *Zygiella* which obviously distinguish the webs, but the fundamental geometric forms are very similar. To the degree that these common features occur, the form of the orb web may be viewed as a convergent adaptation of behavior to the problem of arraying threads in space for trapping airborne prey (Figs. 1, 2).

Nevertheless, the features of the web change throughout the life of the spider. It is useful to examine these changes for clues to the relative contributions of innate

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FIG. 1. A web of an adult female *Argiope aurantia* on the left and an adult female *Araneus diadematus,* as they are rebuilt nearly every day in the 50 x 50 cm laboratory frames. Note the characteristic differences in shape (width over length), fine structure and relative size of center area in the webs of the two species (compare to Table 3).

FIG. 2. The webs of an adult female *Zygiella-x-notata* (on the left) and a subadult female *Neoscona hentzii* are very similar in shape and fine structure, but differ through the free sector with signal thread, which only *Zygiella* builds. Compare these webs to the two in Figure 1.

FIG. 3. Webs built by female *Araneus diadematus* in the laboratory frames at ages 27, 120, and 437 days; all three photographs are enlarged to the same scale, the vertical white lines being originally spaced 20 mm apart. Note the characteristic features like small meshes, relatively short thread, and small catching area in the web built by the young spider, as compared to the larger meshes, longer thread, and large catching area in the web of the adult. The old female builds a rather coarse meshed and irregular web. (Compare to Figs. 4, 5.)

movement programs, physical restraints, and perhaps even the experience of the spider in building as an example of the ontogeny of a specific behavior.

The webs of young and old animals of two different species of spider were measured daily from hatching to death. All observations were performed in a laboratory kept in a cycle of long warm days and short cool nights throughout the 8- to 16-month lifespan of the animals. Individual spiders were kept in aluminum cages large enough to impose no limitation on the web proper, i.e., on the catching zone as distinct from the framing and mooring threads (Witt, 1971). For very young animals, a small wooden frame was also placed in the cage; the animals were not restricted to the frame.

Webs were photographed shortly after they were built each day and were then collapsed by the experimenters; as a rule, the silk was ingested by the spiders and new webs were built the following day. The collapsing procedure does not affect frequency of building; even when undisturbed, the spider dismantles and ingests the web (Breed et al., 1964). We assume that the course of events for laboratory animals is essentially similar to that for animals living outdoors.

The web of *Araneus diadematus* is typical for vertical orb webs: a structure with many radial threads on which is wound a spiral, plainly continuous only toward the center of the web, a more or less isolated hub or platform at the center, and a very variable scaffolding which supports the web proper. While retaining this general structure, the web varies in detail from day to day. Two webs of the same overall size may differ in the areas devoted to the central or spiral zones. Threads may be very evenly spaced or relatively irregular with large open areas. The number of spiral and radial strands, the relatively oval shape of the catching zone, and the total length of thread show different values over time and between spiders. Statistical grouping reduces the variations of short time-course and provides an impression of long-term development of web characteristics (Witt and Reed, 1965).

Age. Some of the age-related changes in

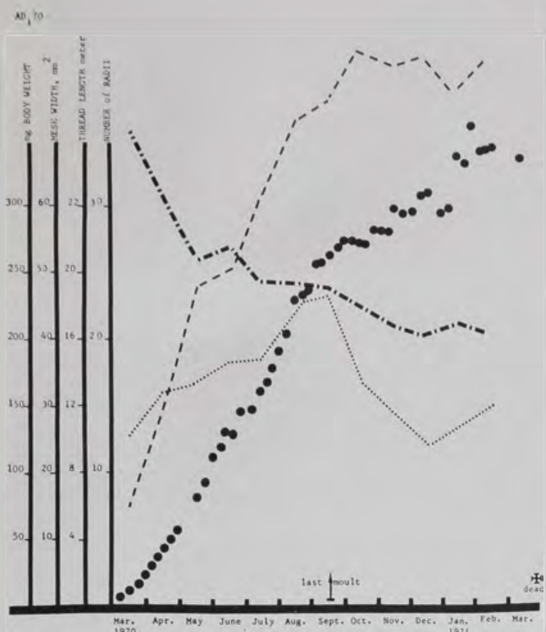

FIG. 4. Body weight and web measures of 35 individual female littermates in Family 1 of *Araneus diadematus* Cl., hatched in the laboratory on the 25th of February 1970. Black, full circles represent mean body weight once a week; dashed line connects monthly means of mesh width in all webs measured in that month; dotted line connects means of all thread lengths; dash-dotted line number of radii. Note the various combinations of web characteristics at different times of life, and their relationship to the time of the last moult or of reaching sexual maturity. (Compare to Fig. 3.)

webs of a single *A. diadematus* female are apparent in Figure 3. A more complete record of web-building ontogeny was obtained from a single cocoon with eggs which hatched in the laboratory in late February (Fig. 4).

The hatchlings were presumably the offspring of a single mating. Over 100 animals emerged from the cocoon, and over the next two weeks traveled short distances back and forth from the cocoon, laying threads and creating a structure with no apparent ordering, resembling a silken sheet. In early March, individual animals drew apart and constructed geometric orb webs which showed all of the characteristic features of the adult web: hub, radii, catching spiral, and frame. At this point, the animals were transferred to individual cages, where they received food and water twice a week. Webs were photographed once a week, after they had been cut the day before, and the spiders were weighed weekly. Similar measures were taken for cocoons hatching shortly before and after this cocoon in order to confirm the generality of the findings for the species.

The mean weight of female *A. diadematus* increases with age in progressive fashion. Since the graph for mesh size (Fig. 4) follows the same general course, weight would seem to be one of the determinants of the texture of the web. The measure "mesh width" refers to the fineness of the network formed in the catching zone by the radial and spiral threads (Witt et al., 1968). A relatively large web with few radial or spiral turns would show a coarse texture. Given equal web size, the greater the number of radial and spiral turns, the finer the texture — the threads being placed at uniform distances. An index of the regularity of that spacing is provided by computing the variance of the

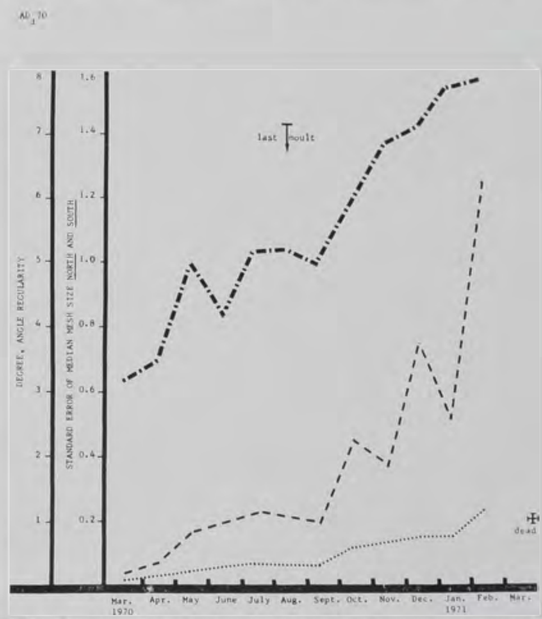

FIG. 5. Regularity measures of all webs built in each month by 35 female littermates hatched in the laboratory on the 25th of February 1970. Dotted line connects means of standard error of median mesh size South; dashed line the means of the same measure in the North part of the web; dash-dotted line the means for angle regularity. Note that all measures indicate increase in irregularity with increase in age, while webs get increasingly wide-meshed. (Compare to Figs. 3, 7.)

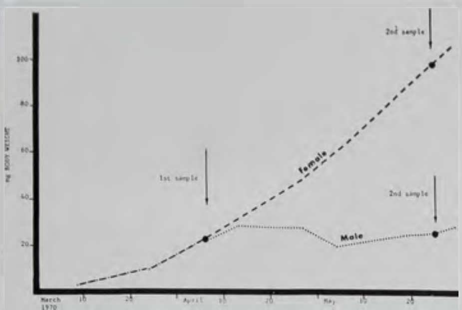

FIG. 6. The growth (body weight) of 35 female *Araneus diadematus* is compared to that of 30 males (littermates) during the first 3.5 months of their lives; vertical arrows indicate days on which webs were measured (*see* Table 1). Note the cessation of growth in males by the middle of April as compared to the continuous growth of females; by the end of May, females weighed about 5 times as much as males.

mesh sizes in several portions of the web (SE median mesh size). In the case of this sample of spiders, the web becomes progressively coarser throughout life until some time after the final molt, when there is also great variability in weight because of the production of eggs. In contrast to Eberhard (1971), who reported differences between "senile virgin's webs and senile nonvirgins" for *Uloborus diversus*, we found in 21 old *Argiope aurantia* female littermates no correlation between changes in web measures and deposition of the egg-cocoon.

Wiehle (1927) states that he always found more radii in webs of young *Araneus diadematus* than in those of old animals. This agrees with the steady decrease in number of radial threads shown in Figure 4, and is in keeping with the progressive openness of the mesh. Figure 5 shows three direct measures of regularity of thread placement: the central angles formed by the radial threads become progressively more variable in size, while the standard error of the mesh also increases, especially in the lower portion of the web.

Thread length – the total linear extent of silk used in building the web – reaches a peak value at about the time of the last molt and then declines. Previous experiments (Christiansen et al., 1962) have shown that the threads of the web become thicker as the weight of the spider is increased (by attaching a weight to the abdomen). The same amount of silk may be employed, but the length of thread is curtailed.

The general effect – which the webs of Figure 3 typify – is that young *A. diadematus* females build small, fine-meshed webs, mature animals large wide-meshed webs, and old animals coarse and somewhat irregular large webs.

Despite this general picture, it can be shown that the regularity of the web is not necessarily a consequence of the size of the spider. Males do not grow to the same size as females (Fig. 6), and although frequency of building drops drastically for males at an early age, they do build a

TABLE 1. *Mean weight and web measures of male and female* Araneus diadematus *littermates 1½ and 3 months after hatching.*

Measurement	Early webs		Late webs	
	14 males	20 females	8 males	20 females
mg Body weight	23.69	26.69	26.41	116.30*
mm Leg length	7.57	7.75	9.75	11.95
cm^2 Spiral area	19.47	19.18	14.98	33.40*
cm^2 Center area	1.64	1.77	1.58	3.15*
m Thread length	11.21	10.98	8.94	14.64(*)
mm^2 Mesh mean	23.58	26.30	25.44	63.14*
SE med. mesh size South	0.021	0.022	0.036*	0.033*

Note that late female webs differ significantly from other webs in 4 measures; while late male and female webs differ from all early webs in the regularity measure.

* Significant difference below P 0.01; analysis of variance.

(*) Significant difference below P 0.05; analysis of variance.

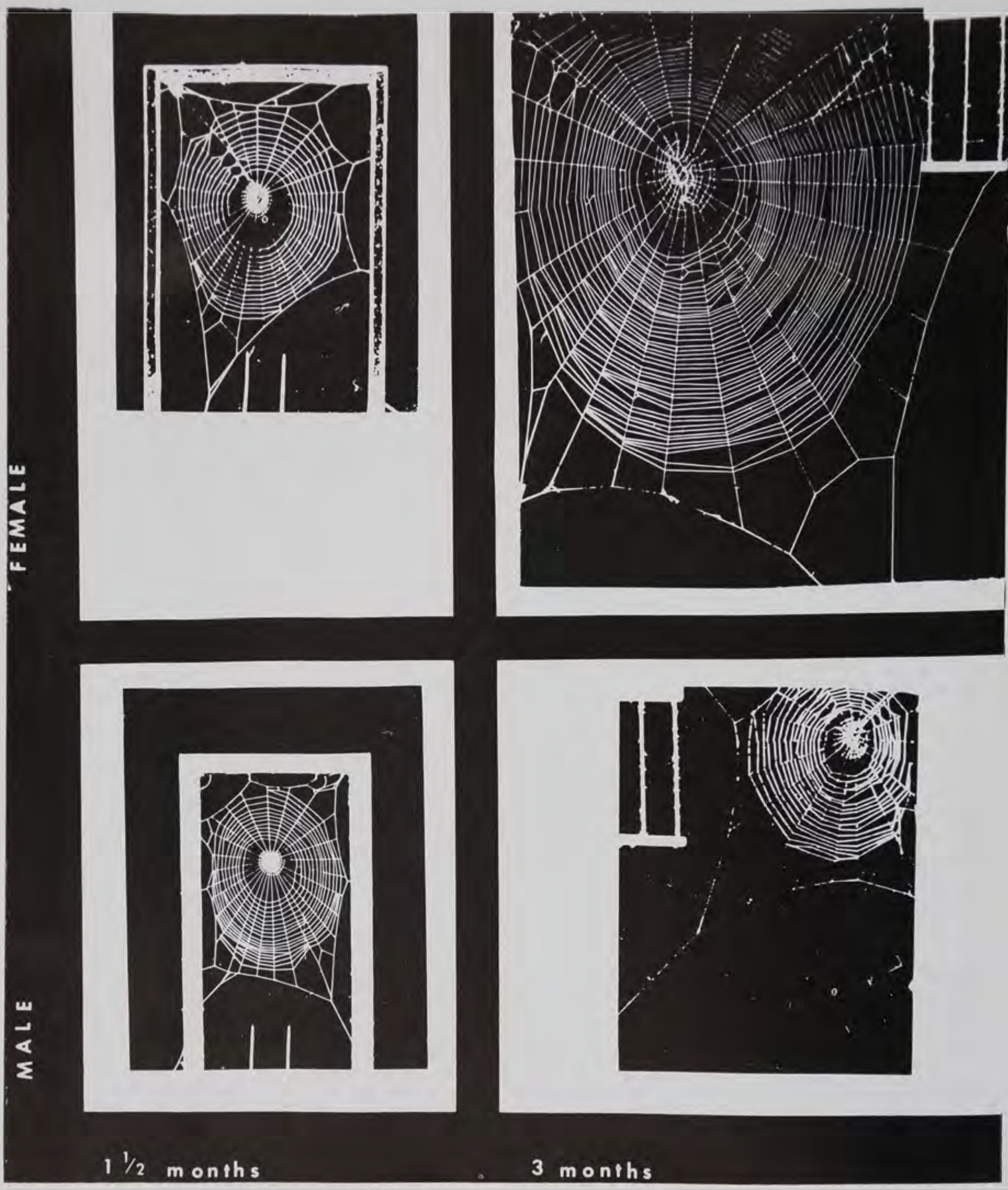

FIG. 7. The upper two webs were built by two female *Araneus diadematus,* the lower by littermate males. When building the two webs on the left, the spiders were 1.5 months old, and the webs on the right were built when they were 3 months old. (Compare to Fig. 6). All webs are reproduced at the same scale. The webs show characteristic features which identify the builders; relatively high irregularity in thread spacing on the right by the more mature animals, and a comparatively large web built with a long thread by the large female. Compare to mean measures in Table 1.

sufficient number to permit comparison with the late webs of females.

Table 1 contains the body and web measures for *A. diadematus* males and females at two periods of life: in April when mass and leg length are equal for both, and at the end of May, when sexual maturity has been reached and the mean body weight of the female spiders has increased fourfold. The males remain at approximately the same mean weight.

Four measures of the web (spiral area, central area, median mesh size, and SE of median mesh – the last a measure of variance) show significant differences between the webs of mature females and all other entries, with the important exception of the variance of the mesh size. In that case, the late male and female spiders show equal irregularity of spacing. A measure not shown in the table – regularity of spacing of the spiral thread – also decreases significantly for the older animals (*see* Fig. 7). These findings suggest that regularity of spacing is related to maturation rather than simply to growth in size. (As examination of the table shows, it is not possible to relate the regularity measures simply to leg length: the older male values occupy a position between the leg lengths of the young spiders and the leg length of the older females.)

It does not appear that this relative decline in web regularity is of a magnitude which decreases the efficiency of the web for catching prey. The spider must move rapidly in any case to seize insects which are entangled by the threads; the important factor for trapping seems to be the area covered by the web, within certain limitation of fineness of the mesh.

Experience. It is often conjectured that experience in web-building serves to modify the form of the web throughout the life of the spider. We have examined this hypothesis by differential treatment of spiderlings from the time of hatching to several months of age (Reed et al., 1970).

Two groups of spiders were kept in narrow glass tubes for 7 or 28 weeks while littermate controls were reared in laboratory cages in which they could build full-sized webs daily. The spiders in the tubes were unable to build though they did emit thread as they moved about in the cramped space. When the confined spiders were released, they built webs significantly smaller than those of their unconfined littermates. In several days, they were constructing webs of normal size.

However, adult spiders with ample building experience also showed reduction in size of the web if confined for only three weeks, suggesting the presence of a limiting factor other than experience. If the silk glands of the confined animals were emptied by pulling silk from the spinnerets each of three days prior to release, the webs built after release were of normal size and detail, if compared to littermates of the same age. Finally, measurement of the rate of silk production in the glands showed that failure to empty the glands had a slowing effect upon synthesis, and led us to the conclusion that relative scarcity of silk rather than of experience accounted for the small webs of the confined spiders. Inasmuch as the webs did not differ in other respects, it appears that experience plays no role in construction of the age-specific web. This conclusion of course does not necessarily apply to other aspects of the spiders' behavior.

Genetic differences. Long familiarity with orb web geometry within a single species encourages the impression that there are individual differences in the form of webs and webs characteristic of littermates of single cocoons. There are signs of individual preference for hub position for instance (Witt, 1956, p. 20) and family characteristics in size (Reed et al., 1970).

A recent study (Rawlings and Witt, 1972), using webs spun by *A. diadematus* females of nearly equal weight, showed a high repeatability for many characteristics of webs spun one week apart by the same spider. This, of course, reflects the joint effects of the unique genetic control of web building behavior for each spider and the composite of all environmental factors influencing the development of their individual behavior patterns. Most notable for the magnitude of their repeatabilities ($>$ 0.5) were the size measures: radii number, number of spirals in the four cardinal directions, frame area, spiral area, center area, and thread length.

Full-sib correlations from the same study provide measures of the similarity of the

TABLE 2. *Mean body weight of females of two species of spiders at the time at which they built webs which were analyzed for similarity in web measures.*

Species	Family	No. individuals in family	Weight in mg at time of building of First web	Second web
Araneus diadematus	I	29	127.1	139.5
	II	18	121.7	137.0
	III	24	119.1	136.5
	IV	4	120.5	138.8
	V	4	115.8	125.3
	VI	1	116.0	135.0
	VII	11	121.1	136.7
	VIII	1	130.0	150.0
Argiope aurantia	I	13	104.2	126.3
	II	18	126.3	132.7

behavior patterns of the full sibs which should be influenced primarily by the genetic factors and to some lesser degree than with repeatability by the common cocoon environment of the full sibs. If one could assume no common environmental influence of the cocoon environment on the web building behavior of the family members, the full-sib correlation measures differing from zero would reflect the presence of genetic variation for that aspect of behavior and imply some degree of genetic control. Again, traits primarily measuring size of web showed the highest full-sib correlations. The fineness, or intricacy, of the web as measured by medium mesh size and mesh width were next in importance. Only five of the 27 traits failed to show significant full-sib correlations.

To extend this analysis one step further, two families of *Argiope aurantia* were sampled in a manner similar to that above. Measurements were taken on webs spun two weeks apart by females of nearly equal weight. The information from *Argiope* was combined with the *A. diadematus* data for further analysis. All measurements of basic features common to the webs of both species were used; stabilimenta of *Argiope* were not included (Table 2).

Two types of analyses were used. The univariate analysis of variance was used to determine the importance of species differences in comparison with differences between families within species. Any indication of species differences must be attributable to a greater genetic similarity of families within species than of families in different species since there should be no common environmental components contributing to the similarities of different families. The second analysis was a multiple discriminant analysis to determine the efficacy with which individual spiders could be classified into the correct family and the correct species solely on the basis of their web building behavior. Again, this is used only as an indicator of the degree of the innate differences in web-building behavior, presumably reflecting differences

TABLE 3. *Web measures showing significant* ($p < 0.05$) *differences between means for two species of orb-weavers (eight families of* Araneus diadematus *and two of* Argiope aurantia, *all females of nearly equal body weight); means are adjusted for remaining body weight differences.*

Web measures	*Araneus diadematus*	*Argiope aurantia*
Radius ratio (north over south)	0.67	0.95
Radius ratio (east over west)	0.73	0.89
Frame area (mm^2)	12905	17051
Spiral area (mm^2)	46459	68683
Center area (mm^2)	3550	7646
Center over spiral area (ratio)	0.085	0.130
Mesh size width (mm^2)	58	88
Relative deviation of spirals (south)	0.38	0.45
Median mesh size—north (mm^2)	51	112
Standard error of median mesh size, north	0.15	0.30

TABLE 4. *Summary of multiple discriminant classification of webs of* Araneus diadematus *and* Argiope aurantia. *Discriminant based on first five families listed, individuals of remaining five families (all known to be* A. diadematus) *classified according to the discriminant function.*

Family	No. of spiders classified into family				
	A. diadematus			*A. aurantia*	
	1	2	3	4	5
1	24	2	3	0	0
2	2	16	0	0	0
3	2	1	21	0	0
4	0	0	0	12	0
5	0	0	0	1	17
6	4	0	0	0	0
7	3	0	1	0	0
8	1	0	0	0	0
9	6	0	5	0	0
10	0	0	1	0	0

in genetic programming.

Based on the univariate analysis, ten measures significantly ($p < 0.05$) discriminated between the two species (Table 3). In all cases, species differences were adjusted for spider weight differences before being tested.

Considering only the shared features of the web, the data show that, despite similar bodily characteristics, the webs of the two species differ in important ways (*see* Fig. 1). *A. aurantia* appears to build larger webs than does *A. diadematus*, the center area, comprising hub and a free zone, being twice as large. The hub is placed more nearly in the geometric center of the web and the texture is larger meshed and more variable, particularly in the northern half, in *aurantia* than in *diadematus*.

The multiple discriminant analysis (using families as categories) was run in two ways. Data from all ten families were used in one analysis to construct the discriminant function. In this case, even though the analysis was terminated when only six measures had been incorporated into the function, 70% of the individual spiders were correctly classified by the discriminant as to family and 99% were correctly classified as to species, i.e., one individual in Family II of *A. aurantia* was misclassified into Family II of *A. diadematus*. The second analysis utilized data from only five families to construct the discriminant (the three families of *A. diadematus* having the largest number of spiders and the two families of *A. aurantia*), and then the twenty-one spiders of the other five *A. diadematus* families were classified according to the discriminant. In this case, 90% of the spiders used in computing the discriminant were correctly classified as to family and all were correctly classified as to species. Further, all 21 of the other spiders were correctly classified as being members of *A. diadematus* (Table 4).

The relatively low rate of error in classification by family and by species encourages the speculation that there are family and species differences, and since experience seems to be unrelated to the construction of the web, that these differences have a genetic basis.

The pattern of the orb web, which can be regarded as a record of a significant portion of the builder's observable behavior, changes in a characteristic way during the life of the spider. Such changes are independent of the spider's prior building experience. There are some features of the web, such as mesh size which seem to be related to growth in size. There are others, such as the regularity of those meshes, which seem to be functions of maturation: the late female webs are measurably different in size only from the late male webs. Other features of the web, thread length for instance, are sensitive to material requirements such as the availability of silk.

While the general pattern of the orb web may be viewed as a successful adaptation to catching airborne prey — and perhaps may be an example of convergent evolution in spiders — specific differences are found even in closely similar webs of different species and different families within species.

While it appears easier to distinguish spider species by their morphological characters, their behavior, at least as measured in the pattern of the orb web throughout life, contains potentially highly discriminable features.

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