

ATTITUDE CHANGE OF *NEPHILA CLAVIPES* SPIDERLINGS (ARANEAE: ARANEIDAE) DURING COMMUNAL LIFE¹

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ABSTRACT

Orientation of the body with respect to gravity by *Nephila clavipes* (L.) spiderlings were scored from the beginning of emergence from the egg sac until the onset of dispersion in the laboratory. Most second instar spiderlings adopted the dorsal-down attitude by the end of the seventh day. A change from dorsal-down to anterior (face)-down attitude—that of spiders living in geometric webs—was apparent on the eighth day, by third instar animals after they had completed the second molt and returned to the communal web. The anterior-down attitude predominated by the time dispersion began.

INTRODUCTION

The orientation of the body of an orb weaving spider with respect to gravity—its attitude—is so commonplace that it often escapes close attention. Bristowe (1958) describes *Araneus diadematus* Clerck as “. . . sitting head downward in the center of her exquisite orb. . . .”; although many familiar books about spiders have pictures confirming this attitude as typical of the orb weaver, there are few descriptions or studies of it. Considering that the web is a vital extension of its builder (cf., Savory 1952:20, Witt 1975), the attitude of the spider in the web center should not remain ignored.

Our attention was drawn to this topic while observing behavior changes associated with the onset of dispersion and geometric web building in golden silk spiderlings, *Nephila clavipes* (L.). Most solitary spiders, including *Nephila*, live together in the egg sac, and commonly thereafter in a tangle of silk for some time after hatching; dispersion is accompanied by changes in behavior (Wilder 1868, McCook 1890, Bristowe 1939, Tolbert 1977). These changes in *Nephila* spiderlings in the laboratory are radical and begin to appear shortly after the second molt (Kimmel and Grant, unpubl. data). Among these changes is the adoption of the head down attitude characteristic of adults at rest, except when posture is adjusted for thermoregulation (Krakauer 1972, Robinson and Robinson 1974). This paper documents the attitude changes that precede dispersion of *Nephila clavipes* spiderlings.

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MATERIALS AND METHODS

Nephila clavipes spiderlings (approximately 425) emerged from an egg sac collected in March 1978 on the South Carolina coast. They formed their communal tangle web, at the top of a 61 x 61 x 9 cm (h x w x d) observation cage containing branches in the laboratory, on 28 March. The cage remained at room temperature (21 - 25° C) and was exposed to a photoperiod (shifted back about 3 hr) of 13 hours of light, from above and a nearby window, and 11 hours of darkness each day. A light mist of water was applied after morning observations and again each evening. Food was not supplied, and the animals were otherwise left undisturbed. Data were collected in 38 scoring periods during ten of the 11 days between beginning of emergence from the egg sac and the onset of dispersion 12 days later (28 March through 7 April, at Davidson, N. C., 35.50° N lat.). Observations were made during the first hour of light each day, and for a longer period in the morning of days 2, 9, and 11, and in the afternoons and/or evenings on days 1, 6, and 8-11.

Spiderlings were selected for scoring from among those not tightly grouped together, in lower parts of the communal mass or on branches during migration. Only animals at rest and whose attitudes could be clearly discerned were scored: a different number of animals was scored each period. Attitude was estimated by eye, with the aid of a protractor when necessary. Any spiderling resting head down, with the anteroposterior body axis no more than $\pm 30^\circ$ from vertical was designated "anterior" attitude ($60/360 = 0.167$ chance of scoring this attitude). Any animal resting with the frontal plane of its body within $\pm 30^\circ$ of horizontal was scored either "dorsal" or "ventral," depending upon whether its dorsum or its venter was closer to the center of the earth ($120/360 \times 0.5 = 0.167$ expected frequency of either attitude by chance alone). Any animal fitting into none of the above categories (that is, with the long axis of its body more than $\pm 30^\circ$ from vertical and its frontal plane more than $\pm 30^\circ$ from horizontal) lay with its side or its posterior surface down and was scored "lateral" (chance frequency 0.5).

Data were combined from observations made during each light period, and the frequencies of each attitude calculated. Daily frequencies were ranked and used in calculating Spearman's rho, or rank correlation coefficient (Conover 1971), and Cooper's sum (Cooper 1975), non-parametric tests for increasing or decreasing trend. Daily frequencies

Table 1.—Daily frequencies of the four attitudes of spiderlings from the time of emergence (day 1) until dispersion began (day 12). The second molt, distinguishing the second instar from the third, began on day 8.

| Attitude | Day, post emergence | | | | | | | | | |
|---------------------|---------------------------|------|------|------|------|--------------|------|------|------|------|
| | 1 | 2 | 3 | 4 | 6 | 7 | 8 | 9 | 10 | 11 |
| | Second instar spiderlings | | | | | Third instar | | | | |
| Ventral | 0.00 | 0.02 | 0.00 | 0.00 | 0.03 | 0.00 | 0.02 | 0.03 | 0.00 | 0.00 |
| lateral | 0.48 | 0.47 | 0.51 | 0.39 | 0.25 | 0.23 | 0.23 | 0.04 | 0.16 | 0.12 |
| dorsal | 0.42 | 0.42 | 0.43 | 0.47 | 0.65 | 0.58 | 0.35 | 0.28 | 0.15 | 0.21 |
| anterior | 0.10 | 0.09 | 0.06 | 0.14 | 0.07 | 0.19 | 0.40 | 0.65 | 0.69 | 0.67 |
| No. observ. periods | 3 | 3 | 2 | 1 | 2 | 1 | 4 | 7 | 5 | 3 |
| No. animals scored | 88 | 64 | 51 | 28 | 60 | 31 | 48 | 68 | 88 | 52 |

of each attitude were corrected for weighting in scoring and the chi-square test for random attitude distribution applied.

Notes were kept on the times of emergence, migration, communal life, molting, and dispersion. *Nephila clavipes* spiderlings usually molt once in the egg sac (Grant, unpubl. data). Spiderlings are termed second instar after completion of this molt. Third instar animals are those that have completed the second molt, which occurs near the communal tangle.

RESULTS

The frequencies of spiderlings found each day in each of the four attitudes are given in Table 1, and are graphed as the distance between lines in Fig. 1. None appears to change through the first three post-emergence days, the period when most of the spiderlings were migrating to form the communal tangle. Frequencies of animals resting in the lateral attitude decreased over the span of the observations. Frequencies of second instar spiderlings adopting the dorsal attitude increased with time: the dorsal attitude was the predominant attitude of second instars by the end of the seventh day, after which the second molt began. Frequencies of second instar spiderlings in the anterior attitude remained low and changed little. Most third instar animals rested in the anterior attitude. The change in attitude from predominantly dorsal to predominantly anterior was abrupt.

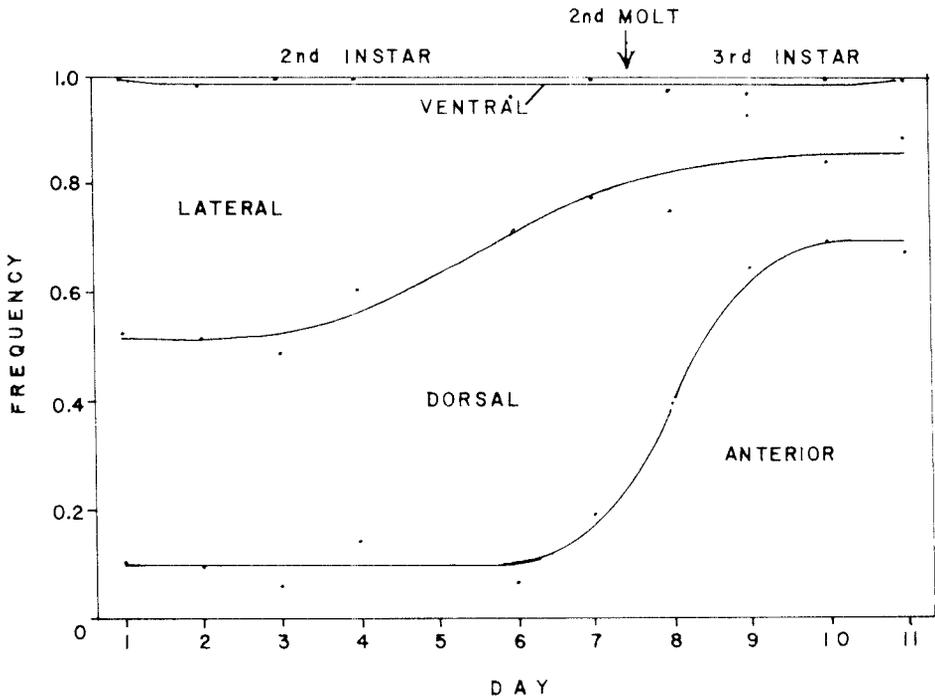


Fig. 1.—Distribution of attitude frequencies on the days between emergence (day 1) and the onset of dispersion (day 12). The four attitude frequencies for each day, from Table 1, are plotted successively on the vertical axis: each frequency is thus represented by the distance between the curves or edges of the graph bounding it.

and clearly apparent on the eighth day, the day third instar spiderlings were first present. Anterior attitude frequencies continued to increase thereafter.

All of these changes in attitude during the second and third instars are statistically significant ($P < 0.05$) by both tests for trend (Table 2). Attitude distribution was random at no time over the course of the observations: chi-square tests for random distribution among the four attitudes, or among the three predominant attitudes, gave P values $<< 0.005$ for each day and for both instars.

DISCUSSION

Nephila clavipes spiderlings undergo changes in attitude during communal life in the laboratory, before the onset of dispersion. Most have adopted the dorsal attitude by the end of the second instar. Third instar spiderlings rest primarily in the anterior attitude. The change in predominant attitude from dorsal to anterior is associated with the second molt. Many spiderlings came to rest head down when they first returned to the communal tangle after completion of the second molt. The attitude change precedes dispersion by at least three days. Numerous observations of subadult and adult *Nephila* confirm both that the anterior attitude is the one typically adopted as they rest in the hubs of geometric webs (Wilder 1868, Robinson and Robinson 1973) and that $\pm 30^\circ$ from vertical are generous limits (Grant and Kimmel, unpubl. observations).

Orb weaving spiders sense and respond to gravity. Newly emergent spiderlings, for example, are negatively geotactic (McCook 1890, Burch 1979) and spiderling attitude is not random in the laboratory. Orb webs are placed in space with reference to gravity (Kaston 1964, Witt *et al.* 1977). Behavioral responses to gravity may be modified by other environmental circumstances, however. Mature *Nephila clavipes* females may face their webs south in winter (Carrel 1978), and alter their postures when exposed to direct sunlight (Krakauer 1972, Robinson and Robinson 1974). Gravity-oriented behavior seems to be an inherited phenotype that the animal can alter in the field for thermoregulation at least.

We are tempted to speculate about the importance of the attitude change described herein to the subsequent appearance of the behavior displayed by orb weavers as they build and use geometric webs, and to the puzzles of phylogenetics, physiology of geotaxis

Table 2.—Spearman's and Cooper's tests for trend applied to ranked daily frequencies of spiderlings in dorsal, lateral, and anterior attitudes. Frequencies ranked in increasing or decreasing order over second instar (2), third instar (3), or the entire eleven days of observations.

| Attitude | Days | Instar | Trend | Spearman's | | Cooper's |
|----------|--------|---------|------------|------------|-------|----------|
| | | | | rho | P | |
| Lateral | 1 - 11 | 2 and 3 | decreasing | -.93 | <.001 | <.001 |
| Dorsal | 1 - 7 | 2 | increasing | +.94 | <.01 | <.001 |
| | 8 - 11 | 3 | decreasing | -.90 | <.05 | .01 |
| Anterior | 1 - 7 | 2 | increasing | +.31 | >.10 | .30 |
| | 1 - 11 | 2 and 3 | increasing | +.86 | <.005 | <.001 |
| | 8 - 11 | 3 | increasing | +.80 | .05 | .01 |

and heliotaxis, and animal locations in webs or retreats. We resist, however, while our experiments continue, and confine ourselves to some critical comments about the present data.

Is it not possible that the attitudes and changes reported here are not geotactic, and are neither genetic nor adaptive: that they reflect reactions to other environmental conditions such as conformation of thread in the tangle, or space available among siblings, or the direction of incident light in the laboratory? *Mallos gregalis* (Simon), a social spider, adopts attitudes in the laboratory that seem to conform to thread arrangement, which in turn reflects the shape of their container (Kimmel, unpubl. observations). The cage top was flat and horizontal in our experiments on *Nephila*. Although the communal web was a three dimensional structure, its major axis was also horizontal. Second instar spiderlings usually hang suspended by their legs. A second instar animal on horizontal threads is apt to hang in dorsal attitude. Some third instar spiderlings remain on the periphery of the group when they return to it after molting, where they may be relatively free to adopt the anterior attitude. Although it appeared that third instars took the anterior attitude regardless of their location in the tangle, no data on location were kept and instances of other attitudes were noted.

Aside from whether the attitude change is imposed by conditions external to the spiderling in the laboratory other than gravity, we wonder about whether it is a discrete change, occurring abruptly after the second molt. No attempt was made to distinguish individual spiderlings in the group; we show changes in attitudes in a population. Any argument about adoption of the anterior attitude being prerequisite for dispersion, orb building, etc., should be buttressed with a description of the variation of attitudes, if any, in which individual animals rest, over time, before they disperse. There is evidence that dispersion is not a sudden, all-or-none event: in the laboratory it seems to begin as a tendency for spiderlings to spread out gradually in the communal web (Burch 1979). Dispersion appears to continue as migratory cycles in *Nephila*, some individuals returning to the group even after having constructed distant geometric webs (Kimmel and Grant, unpubl. data). The attitude change as well might not be discrete, and thus perhaps not initiate the set of behavior changes associated with dispersion.

Finally, observations were made in the laboratory, in artificial confinement, and upon variable numbers of individuals from a single egg sac. Several experiments will be carried out, in the field and in the laboratory, to approach answers to these problems.

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