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Web Orientation in a Golden Orb-web Spider *Nephila clavata* (Araneae: Tetragnathidae)

Tae Soon Park, Joonghwan Jeon, Hang Kyo Lim, Sang-im Lee, and Jae Chun Choe*

Department of Biology, College of Natural Sciences, Seoul National University, Seoul 151-742, Korea

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***Nephila clavata*, a golden orb-web spider, was studied at two different field sites with respect to web size, height, and orientation. A majority of spiders at Site 1 (a band of shrub bush) built their webs parallel or nearly parallel to the edge of the bush. Similarly, at Site 2 (near a pond), most webs were aligned with the shoreline of the pond. Among the possible determining factors for the observed patterns of web orientation, wind and light did not appear important. Instead, the movement direction of insect prey appeared largely responsible. Disproportionately more webs faced outside the bush and toward the pond than inside the bush and away from the pond at Site 1 and 2, respectively. Such trend was more apparent for larger spiders with larger webs.**

Spiders capture prey using a variety of methods. Wandering spiders may actively pursue or ambush prey, while web-building spiders are essentially sit-and-wait predators. The foraging success of web-building spiders is influenced by spider size (Eberhard, 1990), web size (Higgins and Buskirk, 1992; Sherman, 1994), and web placement (Riechert, 1974; Riechert and Tracy, 1975; Chacón and Eberhard, 1980; Rypstra, 1985) as well as specific web parameters such as strength (Lubin, 1986; Denny, 1976), adhesiveness (Opell, 1994), extensibility (Vollrath, 1992), and mesh size (Uetz et al. 1978; Rypstra, 1982; Eberhard, 1986; see also Miyashita 1997 for a more comprehensive list of references).

Web orientation is a parameter that has not been investigated as extensively as others. Studies thus far have focused mainly on the spider's responses to wind (Langer, 1969; Eberhard, 1971; Hieber, 1984) and solar radiation (Krakauer, 1972; Biere and Uetz, 1981; Hieber, 1984; Caine and Hieber, 1987). Wind is considered to cause the greatest structural damage to spider webs and spiders modify the orientation and/or structure of their webs during construction to reduce wind-induced damage (Eberhard, 1971; Lubin, 1973). Spiders show various thermoregulatory behaviors to control insolation, including body orientation (Krakauer, 1972; Robinson and Robinson, 1978; Moore, 1977), web orientation (Tolbert, 1979; Biere and Uetz, 1981), and body reflection (Robinson and Robinson, 1979; Tolbert, 1979).

Web-building spiders require not only a suitable microclimate range but also substrates to which the web can be connected and space in which the web can be seated (Riechert, 1974; Uetz et al. 1978; Wise, 1993). Thus, the orientation of spider webs can also be influenced by the availability and types of substrates, size, and shape of empty space (Eberhard, 1989; Higgins and McGuinness, 1991; Bishop and Connolly, 1992; Higgins and Ezcurra, 1996), and possibly the movement of prey.

In the following account, we examine patterns of web orientation in a golden orb-web spider *Nephila clavata* at two sites that differ in terms of general surrounding, and the composition and arrangement of vegetation. Angles of webs in relation to the surrounding and prey capture rates of webs with different angles are analyzed. Body size of spiders, and various dimensional parameters of their webs such as diameter, height from the ground, and angle from the vertical plane are also recorded.

Materials and Methods

Nephila clavata is a relatively large orb-web spider, common throughout the Korean peninsula (Paik, 1978). A generalized life cyle of *N. clavata* in Korea based on our preliminary observations (Park and Choe, unpub. data) is as follows. Spiderlings begin to emerge from overwintered egg cases in early June, become adults in the period from early September to early October, and lay eggs from late October to early November. The life cycle in Japan is very similar to that in Korea and described in detail by Miyashita (1992, 1994).

This study was conducted from mid-October to early November in 1995 at two sites on the campus of Seoul National University located on the slope of Mt. Kwanak in Korea. Site 1 was a band of shrub (*Ligustrum obtusifolium*) bush along a narrow path (4.3-4.5 m in width and 107 m in length) leading to the Student Welfare Center. The bush was 1.5-2.0 m in height and

* To whom correspondence should be addressed.
Tel: 82-2-880-8158, Fax: 82-2-882-7195
E-mail: jcchoe@snu.ac.kr

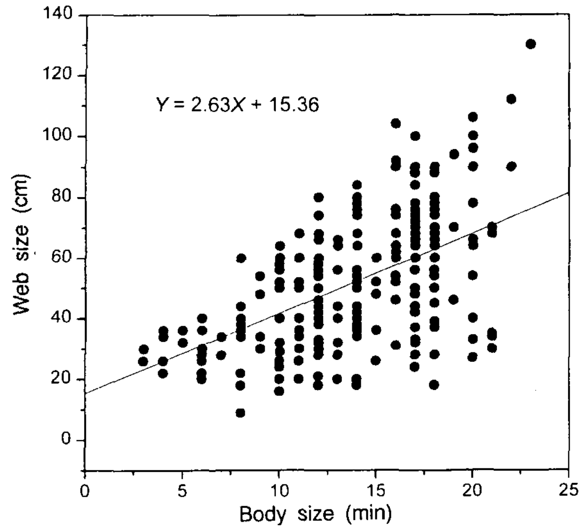

Fig. 1. Relationship between body length and web size of *Nephila clavata*.

1.1-1.4 m in width, and surrounded by acacia trees and grass.

Site 2 was at the pond ("Chahayon"), approximately 350 m away from Site 1. The shape of the pond was nearly a rectangle with the outline of 125 m. The surface area of the pond was approximately 876 m^2. Spider webs were found on shrubs such as *Rhododendron mucronulatum, R. schlippenbachii, Buxus koreana,* and *Syringa* sp. that were sparsely distributed.

The compass orientation of a web was estimated by the angle of the planar web with the direction north. The compass orientation of the bush at Site 1 and that of the shoreline at Site 2 where the webs were found were also measured. The height of a web was measured from the ground level to the web-hub. Vertical and horizontal diameter of planar webs were measured and the web size was estimated as the mean of the two diameters. The degree of tilt of the planar web from the vertical plane was also estimated.

To determine relative prey capture rates of webs with different angles, we removed all prey from 30 webs at Site 1 and 36 webs at Site 2, and counted the number of insect prey captured for a day. We repeated this experiment four times. Particularly small or large prey that *N. clavata* does not eat, such as planthoppers (Delphacidae) of less than 4 mm in length and large lauxaniid flies (Lauxaniidae), were excluded from the count.

Results

The mean body length of *N. clavata* was 12.9±4.9 mm ($\overline{\chi}$±SD, n=226). Adult females (21.5±4.9 mm, n=137) were much larger (one-way ANOVA, $F_{1,\ 202}$= 19.5, P=0.0001) than males (13.5±2.7 mm, n=89). The mean height of webs was 118.4±30.7 cm (n=226) and tilted backward by 15±5.6°. The horizontal diameter of webs (27.74±10.98 cm, n=226) was significantly longer ($F_{1,\ 202}$=12.4, P=0.01) than the vertical diameter (24.09± 7.99 cm, n=226). Larger spiders tended to build larger webs (Fig. 1, r_s=0.61, P< 0.001, n=239) at greater heights (Fig. 2, r_s=0.52, P< 0.001, n=104).

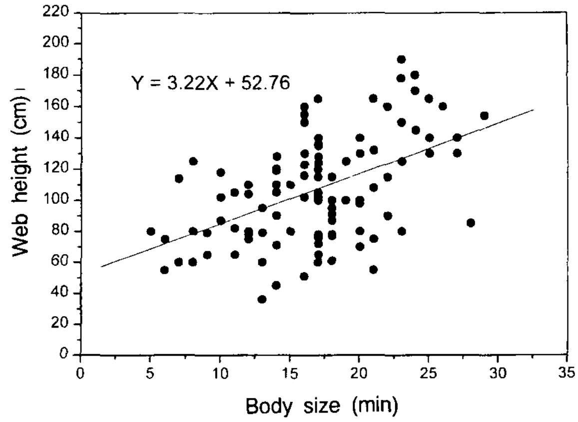

Fig. 2. Relationship between body length and web height of *Nephila clavata*.

Angles of webs in relation to the edge of the bush at Site 1 are presented in Fig. 3. Over three quarters (76%) of all webs (n=273) were facing outside the bush and among these webs a great majority (82.8%) were either parallel or within 30° from the edge of the bush. Compared to the webs with angles of 30-60° and 60-90°, a significantly disproportionate number (Chi-square Test, χ^2=105.4, P< 0.001) of webs were concentrated within the 30° range. Similarly, significantly more (67.4%, χ^2=85.8, P< 0.001) of the webs facing inside the bush maintained less than 30° for the edge of the bush. Overall, 79.2% of all webs were either parallel or within 30° from the edge of the bush, facing the outside or inside.

Fig. 4 illustrates the patterns of web orientation at

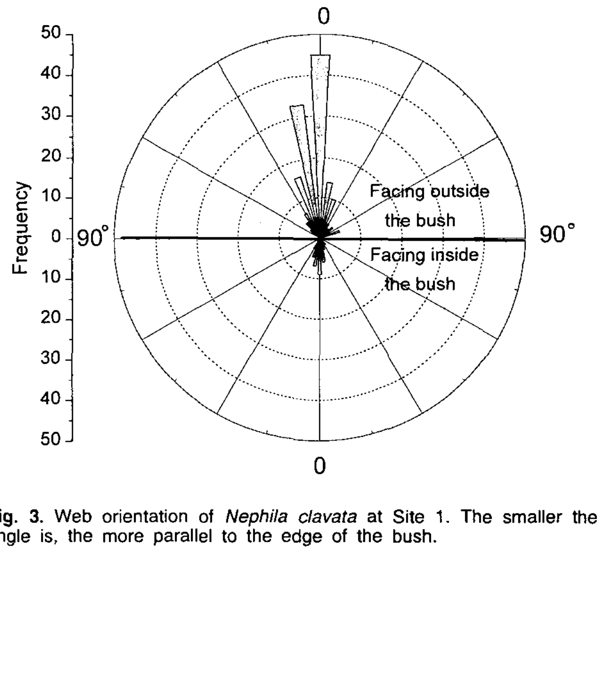

Fig. 3. Web orientation of *Nephila clavata* at Site 1. The smaller the angle is, the more parallel to the edge of the bush.

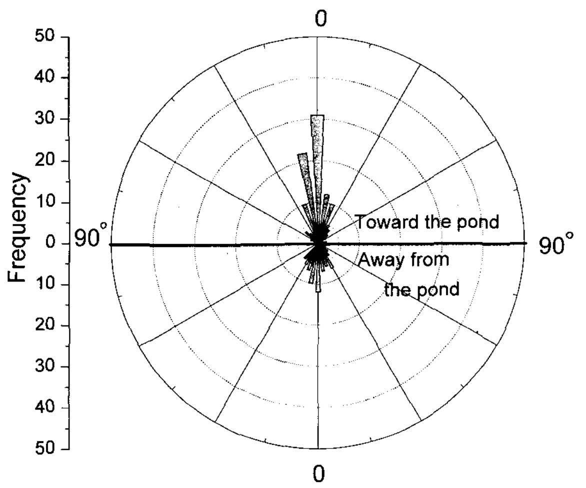

Fig. 4. Web orientation of *Nephila clavata* at Site 2. The smaller the angle is, the more parallel to the shoreline of the pond.

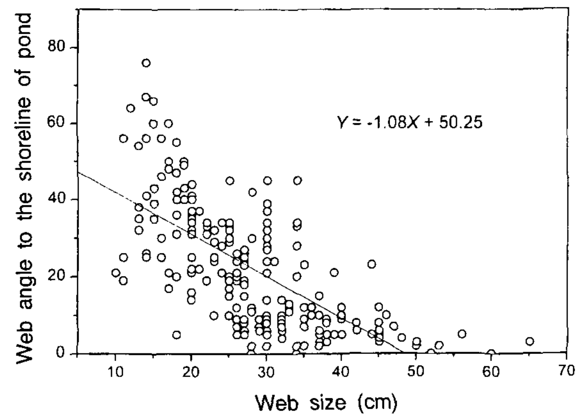

Fig. 6. Web angle to the shoreline of the pond *vs.* web size.

Site 2 by the pond. Of all webs (n=208) facing toward or away from the pond, 70.8% were either parallel or within 30° from the shoreline of the pond. Nearly two thirds (63.7%) of all webs were facing toward the pond and 75.4% of them maintained less than 30° from the shoreline of the pond, which were significantly more (χ^2=68.7, P< 0.001) than those webs with angles of 30-60° and 60-90°. A similar pattern was observed among the webs facing away from the pond. Disproportionately more webs (62.7%, χ^2=49.9, P< 0.001) were within the 30° range.

The tendency to build webs either parallel or nearly parallel with the edge of the bush (Fig. 5, r_s=0.67, P< 0.001, n=224) or the pond shoreline (Fig. 6, r_s=0.60, P < 0.001, n=206) was much more apparent as the web size increased (Fig. 4). No clear patterns emerged with respect to the compass orientation.

The mean number of insect prey captured by spiders at Site 1 (2.23±1.65/spider/day, n=167) did not differ greatly (two-way ANOVA, $F_{1,195}$=1.42, P=0.35) from that at Site 2 (1.98±1.92, n=120). At Site 1, the webs facing outside the bush (2.61±1.84) captured significantly more prey ($F_{1,87}$=10.85, P< 0.01) than the ones facing inside (1.86±1.21). Similarly, at Site 2, considerably more prey were captured ($F_{1,105}$=11.41, P< 0.001) by webs facing the pond (2.37±1.28) than those facing away from it (1.52±1.19).

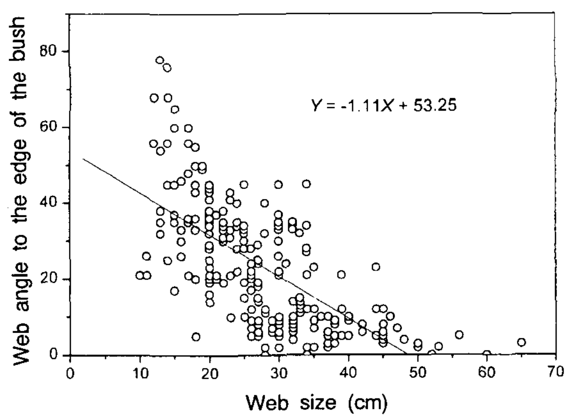

Fig. 5. Web angle to the edge of the bush *vs.* web size.

Discussion

Fitness of web-building spiders depends largely on foraging success, which in turn is influenced by web site selection and tenacity, web size and placement, structural features of the web, spider size, and behavior including social behavior (Shear, 1986; Eberhard, 1990; Uetz, 1992; Wise, 1993). Because silk production and web construction are energetically costly, and golden orb-web spiders (*Nephila*) use their webs as semi-permanent homesites (Miyashita, 1986), where and how to build webs are critically important aspects of their foraging strategies.

Nephila builds a large, complex web consisting of an incomplete, wheel-shaped planar web, and a three-dimensional barrier web above the hub (Foelix, 1996). By building such a web in the bush of shrubs where substrates for the attachment of frame threads are available in many different directions, *N. clavata* could potentially orient its web in any direction. Nonetheless, the present study revealed that *N. clavata* oriented their webs in a predictable fashion.

In addition to the availability of substrates, sufficient space is crucial to web-building spiders (Uetz et al., 1978; Wise, 1993). Web size is often positively correlated with spider size and prey capture rate (Riechert, 1974; Higgins and Buskirk, 1992; Higgins, 1995). Relatively little space was available toward the center of the bush and as a result, almost all *N. clavata* built their webs right along the edge of the bush. Space did not appear to be a critical factor at Site 2.

Web orientation, a parameter that is likely to influence the foraging success of web-building spiders, has been analyzed mainly in terms of structural damage and thermoregulation. Many orb-web spiders build their webs parallel to the direction of the wind to minimize the exposed surface area and thus structural stress imposed on the web (Eberhard, 1971; Lubin, 1973; Waldorf, 1976; Hieber, 1984). We did not measure the directions of prevailing winds in this study. Considering that there are no particular reasons why the wind must blow along the bush or the shoreline of an irregular-shaped pond, however, wind direction does not appear to be a major determining factor for the web orientation of *N. clavata* at the study sites.

Thermoregulation is an important part of life history strategies for orb-web spiders. *Nephila clavipes* living in tropical and subtropical regions are often subject to extreme solar radiation and thus adjust to minimize the exposed body surface by keeping its body axis parallel to sun rays (Krakauer, 1972; Robinson and Robinson, 1974). Behaviorally-mediated thermoregulatory adaptation of orb-web spiders includes the adjustment of web direction. *Micrathena gracilis*, forest-dwelling orb-web spiders, in shaded microhabitats build their webs facing a north-south direction, whereas the webs of those in open microhabitats face an east-west direction (Biere and Uetz, 1981). Overwintering *N. clavipes* in Florida typically orient their webs in an east-west direction to quickly raise their body temperature in the morning (Carrel, 1978). Thermoregulatory adjustment by orb-web spiders affects the amount of time it spends in its web and thus its prey capture rate (Biere and Uetz, 1981).

The webs of *N. clavata* were not aligned with any particular compass directions. When the direction of the bush changed at Site 1, the web orientation changed accordingly. Such a trend was even more obvious at Site 2. Rather than maintaining more or less the same compass direction, the webs were in general parallel to the shoreline of the pond.

An ecological variable that may explain the emerged pattern of web orientation in *N. clavata* is the direction of prey movement. The webs oriented parallel or nearly parallel to the edge of the bush or the shoreline of the pond captured significantly more prey than the more angled webs. The fact that the webs facing outside the bush and toward the pond captured far more prey than those facing inside the bush or away from the pond gives us a clue about the flight direction of insect prey. The finding that larger spiders with larger webs tended to orient their webs more in parallel also suggests that such web placement strategy may be adaptive.

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