

Function and structural variability of the stabilimenta of *Cyclosa insulana* (Costa) (Araneae, Araneidae)

Cornelis R. Neet

Institut de Zoologie et d'Ecologie Animale,
Université de Lausanne, Bâtiment de Biologie,
CH-1015 Lausanne, Switzerland

Summary

Field observations on linear and circular stabilimenta were undertaken on coastal populations of *Cyclosa insulana* (Costa), in Ibiza (Spain). The linear and circular stabilimenta and sticky spiral appear to be independent components of the web. The camouflage function of the linear stabilimentum is confirmed. A comparative analysis of webs built under different degrees of exposure to wind shows that the circular stabilimentum probably has a mechanical strengthening function and that web size is affected by the degree of exposure to air currents. The fact that different independent web components having different functions have been grouped under the common and perhaps misleading term of stabilimentum is emphasised.

Introduction

Several orb-weaving species of the families Araneidae and Uloboridae are known to build a conspicuous white silk structure near the hub of their webs: the stabilimentum. The well-known example of the zig-zag ladder structure of the stabilimentum of *Argiope bruennichi* (Scopoli) is only one of numerous types of stabilimenta that have been described, and which have been classified in two general categories: circular stabilimenta, which include discs spun by some *Argiope* species and concentric loops spun by several *Uloborus* and *Cyclosa* species, and linear stabilimenta, that are found in many species of *Argiope*, *Cyclosa*, and other genera (Edmunds, 1986). Although there are many intermediate forms which render such a classification questionable (Lubin, 1986), it is convenient for the purpose of this paper. Three current theories account for possible functions of stabilimenta (Edmunds, 1986; Lubin, 1986). These are the mechanical strengthening of the web (McCook, 1889; Simon, 1892-5; Robinson & Robinson, 1970, 1973), defence by camouflage (Hingston, 1927; Marson, 1947a, b; Ewer, 1972; Eberhard, 1973; Lubin, 1975; Tolbert, 1975) and advertisement to prevent web destruction by birds (Horton, 1980; Eisner & Nowicki, 1983; Edmunds, 1986). All three theories have received empirical support from various observers (Edmunds, 1986; Lubin, 1986). However, the defensive functions of camouflage and advertising have received the best supportive evidence, as in the case of *Uloborus diversus* Marx (Eberhard, 1973) and *Argiope flavipalpis* (Lucas), where the linear stabilimentum distorts the spider's apparent shape, especially when the spider vibrates its web (Edmunds, 1986; Edmunds & Edmunds, 1986).

In the case of spiders of the genus *Cyclosa*, there is also convincing support for a defensive function (e.g. Gertsch, 1949; Edmunds & Edmunds, 1986), since the

webs of several species bear a linear stabilimentum with added pellets of food debris (McCook, 1889; Hingston, 1927; Wiehle, 1927; Marples & Marples, 1937; Marson, 1947b; Peters, 1953; Levi, 1977; Rovner, 1977; Edmunds, 1986; Edmunds & Edmunds, 1986) or egg sacs (McCook, 1889; Wiehle, 1927, 1928; Kaston, 1948; Levi, 1977), among which the spider stays at rest and which render it very hard to discern.

This defensive function is generally accepted (Edmunds & Edmunds, 1986), but concerns only the linear stabilimentum. The purpose of this paper is to discuss both the linear and circular stabilimenta, and to focus more closely on the function of the latter. So far, the circular stabilimentum of the genus *Cyclosa* has never been interpreted from a functional point of view, except in the case of *Cyclosa insulana* (Costa), where it has been attributed a camouflage function (Marson, 1947b).

Material and methods

The field-work was carried out during the first three weeks of August 1988, in Punta Grossa on the island of Ibiza (Balearics, Spain). *Cyclosa insulana* occurred on the shrubs and bushes that are interspersed with pine trees and form a dense cover on the steeper parts of the rocky coast. The spiders were observed in the field at various times of the day and night along small paths situated in an area quite exposed to coastal winds. Following the paths made it possible to observe individuals in a periodic sequence. This area, situated about 100m above the town of San Vicente, was the main study site. Data were gathered from about 50 individuals, including juveniles and adult females. Adult males were not seen on their own webs. The observations consisted of the description of web building and web removal patterns, description of the stabilimenta, their variability and abundance in the population (some individuals occurring without stabilimenta), and the measurement of web diameter and linear stabilimentum length. Some linear stabilimenta were also sampled in order to examine the debris they contained.

Other series of observations and measurements were made on populations of about 20 individuals in each of two other study sites differing from the main site in their degree of exposure to coastal winds (see below). Statistical analyses consisted of regression analyses, parametric tests for the difference between two means, and *G* tests of independence (Sokal & Rohlf, 1981).

Results

Web building and removal patterns

The individuals of *Cyclosa insulana* observed in the main study site all remained permanently at the hub of their webs. In several cases, it was evident that the spider had been on the same web for several consecutive days, without any web-renewal behaviour. Most individuals remained for 3-4 days on the same web. After this period, web removal occurred, always at night. The new web was then spun the same night, or

during the following night. In the latter case, the spider remained for 24 hours at the hub of a web lacking a sticky spiral but having radii, before building a new spiral. During the three weeks of observation, all the spiders remained at the same web-site, and none was seen to move to other sites to build a new web.

In all cases, web removal and spinning occurred without destroying the linear stabilimentum and the food debris attached to it. The circular stabilimentum, when present, was always destroyed by the web removal process. However, one spider was observed spinning a new circular stabilimentum on a web spun a day or two earlier. In other words, the frame, the spiral and the two types of stabilimenta are built in separate behavioural sequences and may, to a certain extent, be considered as distinct elements of the web. The removal process observed corresponded to the description given by Carico (1986) for *Cyclosa turbinata* (Walck.), except for the fact that *C. insulana* was observed gathering up 7 to 9 radii and associated sticky spiral threads during each removal action, while Carico mentions 3 to 5 radii for *C. turbinata*.

The webs were not randomly placed in the vegetation of the study site. About six species of shrubs were present on the site, but a large majority of webs occurred on only two of these plant species, which were the stiffest and had the largest amount of leaf cover. All the webs observed were placed vertically, and although no measurement of spatial distribution was undertaken, some aggregation was obvious, the spiders being not only selective in web placement, but often occurring in loose groups.

The linear stabilimentum

As mentioned above, the linear stabilimentum is a permanent structure. Linear stabilimenta were observed to have various degrees of structural development. The simplest consisted only of a few pieces of prey debris beneath and above the spider. The most advanced ones consisted of a solid linear structure of closely accumulated debris in which the spider was, for human eyes, difficult to detect. The colours of *Cyclosa insulana* are silvery grey to black with silvery spots (see Chrysanthus, 1961; Locket, 1980), colours that considerably increase the resemblance to the prey debris.

The debris of three linear stabilimenta were examined and found to contain fragments of Homoptera, Diptera and spider exuviae. A striking discovery was a leg of a specimen of the dipteran family Asilidae, probably belonging to the genus *Neomochtherus* Osten-Sacken, a powerful predator which was observed to

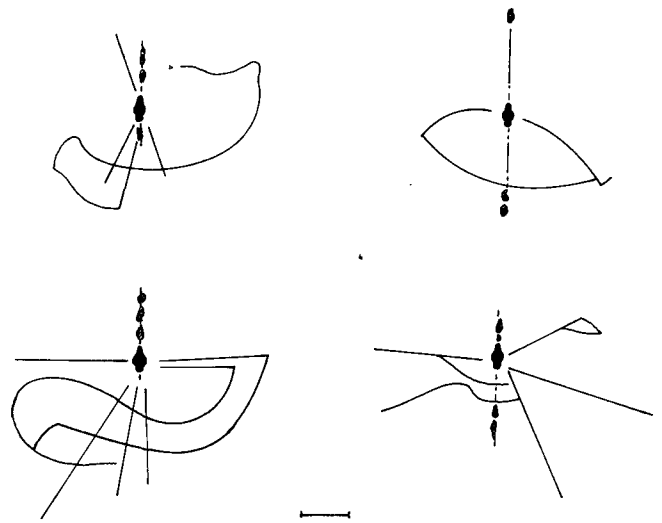


Fig. 1: Four examples of circular stabilimenta observed on webs of *Cyclosa insulana* after a period of strong winds. The radii and sticky spiral are not represented. The circular stabilimentum is shown by continuous curved and straight lines, the linear stabilimentum by pellets and a broken line. Scale line = 1 cm.

pick up other flies from the leaves of bushes where *Cyclosa insulana* was found. Although this *Neomochtherus* sp. was not seen to take spiders, its predatory tactic, which consists of a sudden attack on a resting prey, seems very suitable to attack spiders such as *Cyclosa*. Other potential predators included lizards, which were seen climbing into the bushes to feed on insects, and bats, which were abundant at night and flew frequently just above the bushes. As a defensive device against all these predators, it seems that the linear stabilimentum may well be efficient.

The circular stabilimentum

At first, when observing *Cyclosa insulana*, none of the circular structures first mentioned by Marson (1947b) were found. However, on 5 August, after a stormy night during which there were strong gusty winds, several webs were found to have been destroyed, but others were still present, many of them with circular stabilimenta. As shown in Fig. 1, most of these stabilimenta were rather irregular, completely lacking a geometrical form, except perhaps for a tendency to have a semicircle running across the lower half of the web. As the same individuals had been observed during the preceding days, it was surprising to find that five individuals seemed to have built their circular stabilimentum in response to the very windy weather of the previous 24 hours. In order to test this hypothesis, the

Weather type	With circular stabilimentum	Without circular stabilimentum	G test (df = 1) with case 1
1. Windy (5 August 1988)	10	14	
2. Calm (12 August 1988)	4	23	4.51, $p < 0.05$
3. Calm (18 August 1988)	4	21	3.89, $p < 0.05$

Table 1: G test for independence between the numbers of webs counted with/without a circular stabilimentum, and the type of weather (windy/calm).

number of webs having such a structure among all the individuals found on the study site were counted. Similar counts were also made on 12 and 18 August, i.e. days that had been without wind during the preceding 48 hours. The numbers counted on these two days were compared with the number counted on 5 August by a *G* test for independence, in order to test whether the number of webs including a circular stabilimentum was dependent on the type of weather (Table 1). Since the test rejects the null hypothesis of independence, we must infer that there is some evidence that the construction of a circular stabilimentum is a behavioural response to windy weather conditions. This suggests that this structure may well have a stabilising function. As can be seen from Fig. 1, this conclusion does not seem unreasonable since the silken threads run across the radii of the web, and may therefore strengthen the web and help prevent it collapsing under wind pressures. Moreover, while the linear stabilimentum is independent of the radii and the sticky spiral, the circular stabilimentum is directly attached to all the radii it crosses.

Web design under different degrees of exposure to coastal winds

The results obtained for the circular stabilimentum lead one to ask whether other aspects of web architecture were affected by climatic factors. Therefore, the webs of two other populations exposed to different degrees of exposure to coastal winds were compared. An unexposed population was chosen in a small valley running into the mountains behind the town of San Vicente, an area that is quite well protected from winds, and where there are no air movements at all during calm days. The exposed population was chosen on an open part of Punta Grossa, just above the sea, in a region where winds have the highest impact and where air movements always occur, even on calm days. The comparison was made on August 18, a calm day. The largest diameter of the web and the length of the linear stabilimentum were measured, and the numbers of webs with/without circular stabilimenta were counted (Table 2).

In the unexposed population, no individuals were found with a circular stabilimentum among 22 individuals observed. In the exposed population, 2 were found among 20 observed. As these observations were made on a calm day, this lack of difference is not surprising in view of the observation that this type of stabilimentum occurs during very windy periods. As one may notice, the length of the linear stabilimentum

is independent of the degree of exposure to wind. On the other hand, for the web diameter, a significant difference was found, the webs built in the exposed population being smaller. This result suggests that web diameter and linear stabilimentum length are independent variables. This is confirmed by a regression analysis between them: for the unexposed population we obtain $r = 0.37$, $p = 0.09$, and for the exposed population $r = 0.08$, $p = 0.73$. This supports the conclusion that the circular stabilimentum, the linear stabilimentum and the sticky spiral are independent devices, since these web components show different types of variation with respect to environmental factors.

Discussion

The defensive function of the linear stabilimentum is supported by several studies (see Edmunds & Edmunds, 1986). The camouflage effect is obvious and, as mentioned above, there are several potential predators which may attack the spider directly and, therefore, this defence system may well be efficient. The linear stabilimentum of *C. insulana* does not seem to have any stabilising function, and the advertising function, although perhaps applicable to bats, does not seem to hold in this case for birds, as there were relatively few on the study site. Observations on the linear stabilimentum clearly showed that the pieces of debris are fixed together with the same type of silk that is used to build the stabilimentum itself. Although debris and silken structure may vary in amount and may appear relatively independent (Marples & Marples, 1937), it does not seem that these structures should be considered as independent types of stabilimenta, as Rovner (1977) suggested.

Since the linear stabilimentum was observed to be permanent and independent of web renewal, and since the observed individuals were sedentary, some with very ornate stabilimenta, indicating long-term residence, it seems acceptable to interpret the linear stabilimentum as analogous to the retreat structure of other Araneidae. There is, at least, no argument against this hypothesis. It should be stressed that although in *C. conica* (Pallas) the linear stabilimentum is not found on every web (Marples & Marples, 1937), on the webs of *C. insulana* it was almost always present.

The circular stabilimentum appears to be a quite different structure from the linear one. It is ephemeral and is certainly involved with the mechanical stability of the web under strong wind conditions. Interestingly, web diameter also varies according to the wind factor.

	Circular stabilimentum		Web diameter ± S.D.	Length of linear stabilimentum ± S.D.
	With	Without		
1. Unexposed to wind ($n = 22$)	0	22	14.4 ± 4.47	2.25 ± 1.87
2. Exposed to wind ($n = 20$)	2	18	11.7 ± 3.44	2.25 ± 1.29
Statistical tests	<i>G</i> test: N.S.		$t = -2.18$, $p < 0.02$ ($df = 40$)	$t = 0.01$, $p = 0.50$ ($df = 40$)

Table 2: Comparison of numbers of webs with/without a circular stabilimentum, web diameter (in mm) and linear stabilimentum length (in mm) between populations differing by their degree of exposure to wind and coastal air currents.

It should be mentioned that habitat structure parameters were not measured, and it is assumed that the slight differences in vegetation structure between the study sites were not important in determining the differences found in web diameter. While the construction of the circular stabilimentum appears to be an emergency behaviour (occurring when needed), the results suggest that smaller webs in areas exposed to coastal winds may be a somewhat more effective response to daily air movements. In a different context, it has previously been observed that the orb-weaver *Tetragnatha extensa* (L.) reduces its web diameter under unfavourable atmospheric conditions (Neet, 1986). However, to make a clear assessment in such cases of web size reduction in response to environmental factors it would be necessary to undertake appropriate field experiments.

The structural variability of the circular stabilimentum is illustrated in Fig. 1 and by Marson (1947b). The structures observed here correspond closely to the descriptions of Marson, who distinguished diametrical lines of debris (continuous lines) and diametrical lines of pellets (discontinuous lines). This distinction seems to be of doubtful validity, since these cases were observed here to be extremes of a continuum of variability. Marson also distinguished central pads associated with the circular stabilimentum. The present observations fit this description to a certain extent, but large circular platforms at the hub were not observed, as they were by Marson.

To conclude, it is emphasised that the results presented here offer some good arguments in favour of a mechanical function of the circular stabilimentum of *Cyclosa insulana*. It is also shown that web components differing in function and in structure can be distinguished and, therefore, they should not be grouped under a common and misleading term of stabilimentum. The term stabilimentum is appropriate for the circular device. For the linear one, a term such as camouflage silk would seem to be more correct. Finally, it is also shown that, as well as factors such as crowding and prey density (Gillespie, 1987), climatic factors are also of importance in influencing web size and design.

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