One spider a leaf: competition for web-sites in *Nephila maculata* spiderlings.

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宮下 直・深見 理・島崎 彩¹⁾: 一枚の葉に一匹のクモ:
オオジョロウグモの子グモにみられる造網場所をめぐる競争

Abstract Spiderlings of the orb-weaver *Nephila maculata* frequently build webs on a large leaf surface such as *Farfugium japonicum*. In our observations and removal experiment, the spiderlings showed (1) uniform distribution with respect to leaves, i.e., one spider a leaf, (2) high preference for “deep” leaves which were limited, and (3) higher immigration rate onto leaves from which spiders were removed. These provide evidence of intraspecific competition for web-sites, a phenomenon rarely reported in orb-web spiders.

Introduction

Most orb-web spiders construct webs between twigs, between leaves, or between rocks. To our knowledge, the only orb-weavers building webs regularly on a leaf surface is *Araniella* spp (Chikuni 1989). Recently, we frequently found a spiderling of *Nephila maculata* living on a large leaf such as *Farfugium japonicum* (Compositae) and *Alocasia macrorrhiza* (Araceae) in Okinawa, southwestern sub-tropical island of Japan.

This distinguishing characteristic enables us to easily estimate the availability of web-sites because the leaf surface of particular plant species is a unit of potential web-site. Since abundance of such large leaves seemed to be limited, we expected intraspecific competition for web-sites.

To determine whether such competition existed, we addressed the following three questions using the leaves of *F. japonicum* as web-sites, 1) Do spiders show a uniform distribution with respect to leaves? 2) Do spiders prefer a particular type of leaf? 3) Does removal of spiders from the leaves induce immigration of other individuals?

Materials and Methods

In Okinawa, *N. maculata* emerges from the egg cocoon around March and matures in July or August. During their early stage, spiderlings of up to 5 mm body length frequently build webs on a leaf. Individuals we used in April 1998 were early instars, about 2–3 mm body length, that had been molted most probably twice or three times.

Observations and a removal experiment were performed in the Ryukyu University Forest at Yona located northeastern part of Okinawa Island. Spiderlings of *N.*

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Fig. 1. Three parameters measured for the leaf of *Farfugium japonicum* and the location of the spider web.

maculata were found on leaves of *F. japonicum* and *A. macrorrhiza*, but rarely on other leaves. Although some spiderlings construct webs between branches or leaves, the number of them was much lower. *F. japonicum* was the main web-site, and we recorded the number of spiders on each leaf of this plant. To know which type of leaf was preferred, we measured three parameters for leaves with and without spiders: length, width, and depth (Fig. 1).

Removal experiment was conducted on April 2, 1998. For 37 leaves with spiders, all the spiders and their webs were removed and subsequent immigration was recorded on the following two days. Similarly, for 27 leaves without spiders, immigration was recorded on the following day.

Results

Most leaves of *F. japonicum* had one or no spiderling of *N. maculata* (Fig. 2). The distribution was non-random ($\chi^2=8.81$, $p<0.02$) and showed a uniform pattern (Morisita's $I\delta=0.145$). This suggests that the capacity of each leaf is nearly one individual, which appears to be maintained by intraspecific competition for web-site.

The presence or absence of spiders was not related to the size of leaf (length (cm): 20.4 ± 4.1 with spider, 20.3 ± 4.0 without spider (mean $\pm$ SE), $F=0.002$, $p=0.967$, width (cm): 22.6 ± 4.7 with spider, 21.2 ± 4.5 without spider (mean $\pm$ SE), $F=0.814$, $p=0.373$). However, leaf depth was much larger for the leaf having spiders (Fig. 3, $F=54.9$, $p<0.001$). As the leaf depths with and without spiders overlapped only slightly, it appears that most leaves available for web building had already been occupied by spiders.

Thirty-eight percent of leaves from which spider had been removed was occupied by immigrants on the following day and 43% on 2 days later. Contrarily, rate of immigration on leaves having no spiders on the previous day was only 7%. This also indicates spiders compete for web-site of better quality.

Fig. 2. Frequency distribution of the number of *N. maculata* spiderlings with respect to one leaf. Bars and plots indicate actual and expected frequencies, respectively. The expected values are calculated from Poisson distribution.

Fig. 3. Distribution of leaf depth of leaves with and without *N. maculata* spiderlings.

Discussion

We found several lines of evidence for the existence of intraspecific competition for web-site: 1) uniform distribution with respect to leaves, 2) high preference for “deep” leaves, and 3) higher immigration rate onto leaves from which spiders were removed. Intraspecific competition for web-site has been reported for the funnel web spider

(Riechert 1981) and the sheet web spider (Schaefer 1978, Leclerc & Blandin 1991, Samu *et al.* 1996), but seldom reported for orb weavers (see Wise 1993). Both funnel and sheet weavers make webs at two-dimensional space, so the chance of the encounter between individuals may be higher compared to orb-weavers that normally construct webs at three dimensional and more open space.

Obviously, web-site of *N. maculata* spiderlings is two dimensional rather than three, which is unusual for orb-weavers. Moreover, the number of leaves suitable for making webs seem to be limited because large leaves with a particular depth are restricted mostly to *F. japonicum* and *A. macrorrhiza* in the study field. These two unique characteristics make intraspecific competition important that is rarely found in other orb-weavers.

The reason for one spider a leaf seems simple. The center of the web is located mostly at the intermediate point of leaf width where leaf depth was nearly maximum. Since the mean web diameter (8.5 cm) spans more than one-third of leaf width, it seems hardly possible to make another web at the outer part of the leaf surface where leaf depth was small. This indicates that the leaf of *F. japonicum* has a capacity for just one spider.

Rapid immigration in the removal experiment provides further evidence for limited web-sites, consistent with the competition hypothesis. However, the percentage of leaves occupied by spiders did not increase on the second day. It is likely that most spiders searching for suitable web-site near-by settled on the first day following removal.

The advantage of using a leaf as a web-site is not clear, but here we propose three possible explanations. One is a structural stability within a leaf relative to between twigs or leaves. For example, imagine two types of webs, one constructed between leaves of different plants and the other on a leaf. The first type seems more vulnerable to wind damage because each leaf may move with a different velocity. Making a web on a leaf could save additional costs of web construction due to the wind damage. There might be other advantages: prey capture rate might be higher and mortality rate due to predation might be lower on a leaf surface. All of the three explanations can be tested in the field, which will uncover the adaptive significance of the interesting web-site selection in *N. maculata*.

Acknowledgments

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摘 要

オオジョロウグモの子グモは頻繁にツワブキなどの大型の葉の表面に造網する。著者らは観察および除去実験により、(1)クモは一枚の葉を単位とした一様分布を示し、(2)数の限られた「深い」葉に対する選好性が高く、(3)個体を除去した葉への移入率が高いことを明らかにした。これらは、円網種ではほとんど報告例のない、造網場所をめぐる種内競争の存在を示すものである。

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