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Effects of Web Design on the Prey Capture Efficiency of the Uloborid Spider *Octonoba sybotides* under Abundant and Limited Prey Conditions

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ABSTRACT—The influence of web design on prey capture efficiency was investigated in the orb-webs of *Octonoba sybotides* under different prey conditions (abundant and limited). The insects captured by artificial traps under limited prey conditions were smaller than those captured under abundant prey conditions. *O. sybotides* webs with spiral stabilimenta (SP webs) have a narrower mesh and a larger catching area than webs with linear stabilimenta (LN webs). Previous studies have shown that the form of the stabilimentum is changed in response to the internal energetic state of individual spiders. Food-deprived spiders tend to construct SP webs, and food-satiated spiders tend to construct LN webs. The total thread length of SP webs is significantly longer than that of LN webs; so food-deprived spiders seem to invest more energy in foraging than do satiated spiders. When prey was abundant, prey sizes and capture rates for SP webs and LN webs were similar. LN webs may have an advantage over SP webs in prey capture when prey is abundant, because SP webs appear to be more costly than LN webs. On the other hand, SP webs caught more prey than LN webs under limited-prey conditions, when the prey was smaller than under abundant-prey conditions. The average size of prey captured on SP webs was smaller than that on LN webs; SP webs seem to catch more prey than LN webs by catching smaller prey efficiently in prey-limited conditions. Since the food-deprived and food-satiated conditions of spiders in the field may correspond to the potential prey abundance in their habitat, *O. sybotides* seems to change its web dimensions in order to capture prey efficiently under different prey conditions.

INTRODUCTION

Optimal foraging models predict that the breadth of diet and the intensity of the foraging effort of animals change in response to their energetic state (Charnov, 1976). In general, animals' diet under food-deprived conditions is more varied, and includes less profitable prey, while under food-satiated conditions they selectively catch more profitable prey (Krebs, 1978; Stephens and Krebs, 1986).

Some studies of orb-web spiders have shown that the spiders change the structure of their webs in response to energy gain and expenditure. Food-deprived spiders tend to increase their investment in web threads. The increase in the amount of thread is related to changes in web dimensions: a larger catching area or narrower mesh (Herberstein *et al.*, 1998; Higgins and Buskirk, 1992; Sherman, 1994). It is likely that a larger catching area increases the prey capture efficiency (Chacón and Eberhard, 1980; Herberstein and Elgar, 1994). Herberstein *et al.* (1998) also found that food-deprived *Argiope keyserlingi* constructed webs with a larger catching area and a narrower mesh. They suggested that the narrower mesh increases the spiders' range of prey by including smaller, less-profitable insects. Although some previous studies have not shown a clearly positive association between mesh and prey size among species (Nentwig, 1983; Uetz *et al.*, 1978), a narrower mesh appears to be more effective in catching smaller flying insects (Edmunds, 1978; Murakami, 1983). Sandoval (1994) demonstrated that *Parawixia bistriata* spins webs remarkably dimorphic in mesh size that are correlated to the mean prey size available. However, no study has examined the effect of changes in web structure in response to the energetic state of the spider on prey capture success.

Octonoba sybotides is an orb-web spider that is widespread in eastern Asia. The spider is known to add distinct linear and spiral forms of stabilimentum to its web (Watanabe, 1999a; Watanabe, 1999b). The linear stabilimentum consists of a mat of white silk laid in a line along the radii. The spiral stabilimentum, on the other hand, consists of a silky mat laid in circular loops at the hub. The two forms of stabilimentum correspond well to the energetic state of the spiders: food-satiated spiders tend to form linear stabilimenta, whereas hunger induces spiders to form spiral stabilimenta (Watanabe, 1999a; Watanabe, 2000a). The catching area and mesh size

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of the two types of web are different: the catching area is larger and the mesh is narrower in webs with spiral stabilimenta (SP webs) than in those with linear stabilimenta (LN webs) (Watanabe, 1999b). These facts suggest that *O. sybotides* will construct an SP-web with a larger catching area and a narrower mesh when food deprived. It is possible that the larger catching area and narrower mesh increase the efficiency of prey capture or increase the range of prey. In addition, I experimentally examined the influence of web type on the speed of a spider's response to prey (Watanabe, 2000b). The results indicated that web type, rather than the spider's energetic condition, influences the response speed to prey of different sizes. The spiders seem to adjust their prey selection in response to their energetic state, regulating both web structure and prey-catching behavior by modifying their web design.

Octonoba sybotides does not change its web site frequently. Like other uloborid spiders (see, for example, Eberhard, 1972), *O. sybotides* tends to repair sections of its web and infrequently renews the whole web and the form of stabilimentum before dawn (Watanabe, personal observation). When the spiders become food-deprived therefore, it is because prey levels in their habitat are low, rather than a failure to find prey-rich sites. Therefore, a SP web, which is strongly associated with a deprived energetic state in the owner spider, may be effective for catching prey in a prey-limited environment. Previously, I compared the prey catching rate of the two types of web in the field, and found no numerical difference in prey interception (Watanabe, 1999b). However, I did not examine the effect of the abundance of potential prey or prey size distribution. In this study, I examined whether there are differences in the prey capture efficiency and size distribution of captured prey between the two types of webs (SP webs and LN webs) under abundant and limited prey conditions.

MATERIALS AND METHODS

Field observations were conducted at the Kyoto University Botanical Garden, in Kyoto basin, Japan, from early May until mid September in 1999. A census area (8 m×1 m) was established, in which a hundred flowerpots (a truncated cone type: 12 cm high with a rim 14 cm in diameter and a bottom 8 cm in diameter) were placed on a wooden stand (0.5 m high) in 4 lines and 25 rows. Each flowerpot was filled with soil. Spiders constructed their horizontal orb-webs between the flowerpots.

These spiders catch prey struggling on their webs just by wrapping the prey up and do not use poison. When the web intercepts a new prey while a spider is ingesting a captured prey, the spider will dash to the prey and wrap it. However, the spider then leaves the new prey on the catching area and returns to the hub. After finishing ingesting its prey, the spider usually returns to the second wrapped prey and begins to ingest it. Although the spiders catch prey insects during both the day and night, they appear to be diurnal foragers and catch prey insects mainly during the daytime (Watanabe, personal observation). To compare the prey capture rates of the two types of web, I observed the number of prey trapped on the webs or consumed by mature and immature (total length>4.0 mm) spiders between 1430 and 1600 h, at intervals of at least 2 days. The prey interception rate was calculated as the number of insects per web per census. Wrapped prey insects left on the web were collected in separate plastic cases, and brought to the laboratory to measure body length. Insects that were trapped and had died on webs but had not been wrapped by the owner spider were not considered captured prey. Such insects are not likely eaten by *O. sybotides*, because the spider usually does not recycle (re-absorb) the web threads and may not consume the insects trapped on web threads. Therefore, such insects should not to be counted as prey.

Web dimensions (the mesh size, catching area, and total thread length) were estimated following the method of Sherman (1994), with a modification. To estimate the total length of the radial threads, Sherman (1994) used $NR\times(RAD_w–RAD_h)$, where NR equals the number of web spokes (radial threads), and RAD_w and RAD_h equal the average radius of the web and hub, respectively. However, I used $NR\times RAD_w$, because there was no reason to subtract RAD_h from RAD_w.

I estimated daily prey abundance in the study area by setting five artificial sticky traps in a linear array at 1.5-m intervals. The sticky traps were made of flexible, semitransparent plastic sheets, treated with Tanglefoot on both sides and stretched over hard black plastic frames (5×10 cm). Each trap was leaned against a flowerpot at a 45° angle. The five traps were set at 1000 h and collected at 1700 h,; trapped insects were counted and their body lengths were measured in the laboratory. I did not count insects that were smaller than 0.5 mm, because *O. sybotides* of the size classes observed (total length>4.0 mm) are unlikely to attack such small prey. Insects with a body length of less than 0.5 mm were never found among the wrapped prey on the webs.

Although many censuses were conducted through the study period, analysis of the data was limited by changes in the number and size of spiders over the study period. I used the data from the days when there were at least 12 spiders (total length>4.0 mm) on each type of web to compare the prey capture rate between the two types. There were data for 54 days.

RESULTS

The prey capture rates of both the SP and LN webs (CR-S and CR-L, respectively) were positively correlated to the total number of insects captured in the five artificial traps (r^2= 0.376, $p<0.001$ and r^2=0.611, $p<0.001$, respectively) (Fig.

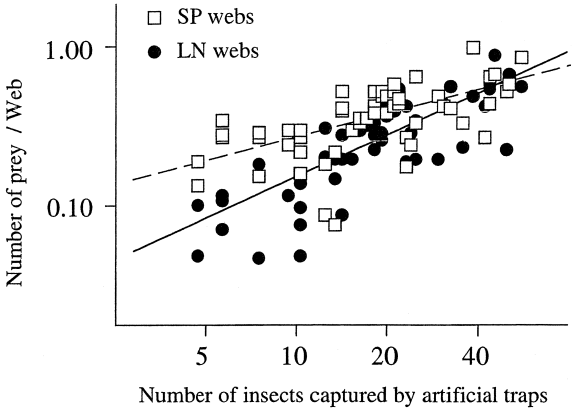


Fig. 1. Relationship between the number of prey captured by artificial traps and the number of prey per web per census. The lines are fitted by the linear models y=–2.497+0.496x (r^2 = 0.376, $p<0.001$) for SP webs and y=–3.1921+0.87x (r^2=0.611, $p<0.001$) for LN webs. The slopes of the two lines are significantly different. Both axes have log scales.

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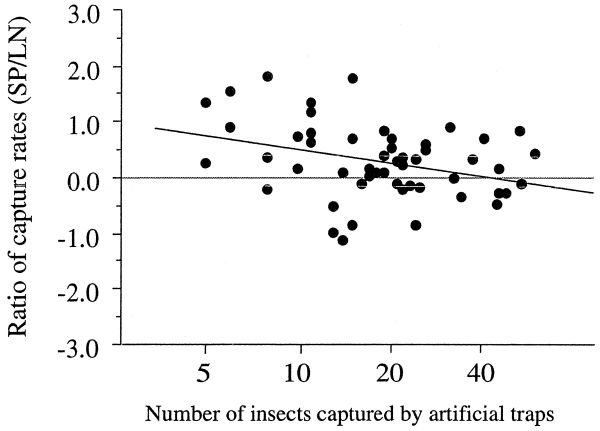


Fig. 2. Relationship between the number of prey captured by artificial traps and the ratio of the capture rates of SP and LN webs. The line is fitted by the linear model $y=1.334–0.355x$ ($r^2=0.118$, $p<0.02$). Both axes have log scales.

1). The slopes of the two lines were significantly different ($F = 8.178$, $p<0.01$). The ratio of the capture rates of the SP and LN webs (CR-S / CR-L) was negatively correlated to the total number of insects captured by the traps ($r^2=0.118$, $p<0.02$) (Fig. 2).

To investigate whether the differences in average insect size in the environment were responsible for the difference in the prey capture efficiencies of SP webs and LN webs, I analyzed the size distribution of the prey captured by each type of web under different prey abundance conditions. Since the daily number of prey collected from webs was small, the daily samples were pooled into three groups (limited, medium, and abundant), based on the number of insects captured by the sticky traps. Days were considered 'limited' (19 days), 'medium' (17 days), and 'abundant' (18 days) when from 5 to 14, 15 to 22, and 23 to 58 insects were trapped, respectively (Table 1). To make subsequent analyses concise, I analyzed only the data for days that prey was abundant or limited. The results including the data from medium days do not affect the following conclusions.

Table 2 shows the dimensions of each type of web (SP and LN webs) under the two different prey conditions (abundant and limited). None of the three characteristics (mesh size, catching area, and thread length) of the two types differed between the two prey conditions (Mann Whitney U-test: $p>0.10$). The mesh of the SP webs was significantly smaller than that of the LN webs under both prey conditions (Mann Whitney U-test: $p<0.001$). The catching area of the SP webs was significantly larger than that of the LN webs under both prey conditions (Mann Whitney U-test: $p<0.001$). The total thread length of the SP webs was significantly longer than that of the LN webs under both prey conditions (Mann Whitney U-test: $p<0.001$).

Table 1. Distinction of day conditions. Abundant, medium and limited refer to the prey abundance levels estimated by five artificial traps set at the study site.

	Prey abundance		
	Limited	Medium	Abundant
Number of days observed	19	17	18
Number of prey trapped per day (Mean±SD)	9.7±3.1	18.7±2.5	37.0±11.4
(Range)	(5–14)	(15–22)	(23–58)

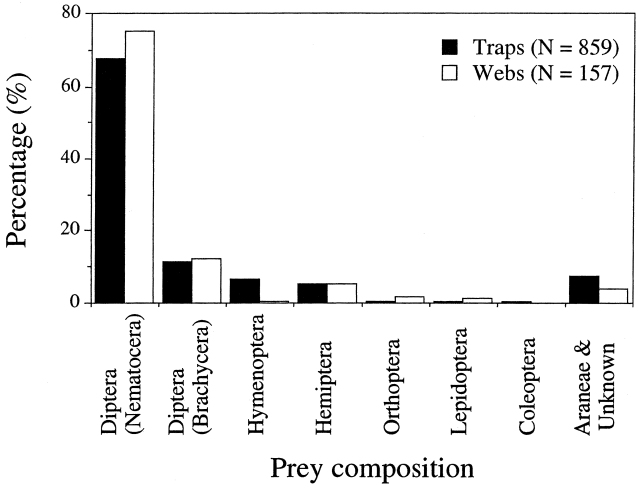


Fig. 3. Taxonomic composition and relative frequencies of insects captured by artificial traps and spider webs.

Table 2. Mean (±SD) web characteriestics for SP–webs and LN–webs under abundant and limited prey conditions.

	Web types		Mann Whiteny test	
	SP	LN	Z	P
(a) Abundant				
Number of webs	228	225		
Mesh size (mm)	2.5±0.4	2.9±0.4	–10.62	p<0.001
Catching area (cm^2)	233.7±84.1	185.2±87.8	–5.84	p<0.001
Total thread length (cm)	1273±293	894±273	–11.94	p<0.001
(b) Limited				
Number of webs	223	224		
Mesh size (mm)	2.5±0.3	2.9±0.4	–11.88	p<0.001
Catching area (cm^2)	243.4±88.8	188.2±66.8	–6.78	p<0.001
Total thread lenth (cm)	1334±322	932±214	–12.38	p<0.001

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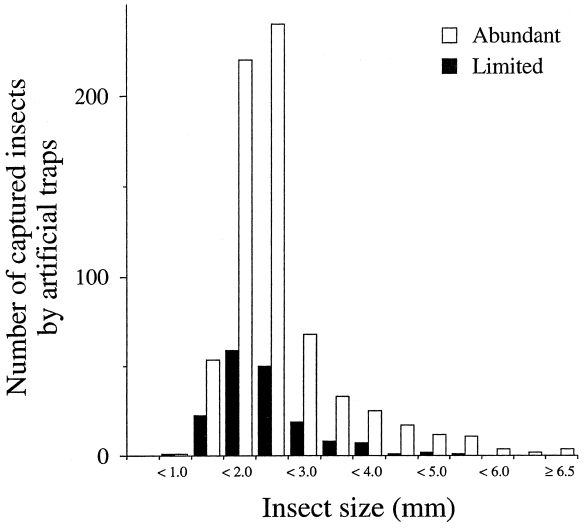


Fig. 4. Size distribution of insects captured by artificial sticky traps on prey-abundant and prey-limited days (n=689 and 170, respectively). The insects captured on prey-limited days were significantly smaller than those captured on abundant days.

I classified insects captured at the artificial traps and spider webs according to their order (Fig. 3). Prey found at spider webs consisted mainly of flying dipteran insects (Nematocera plus Brachycera>85%). The artificial traps also captured mainly dipteran insects (Nematocera plus Brachycera>75%). In both cases, over 85% of the Diptera were Nematocera.

The insects captured by artificial traps on prey-limited days were significantly smaller than those captured on prey-abundant days (Mann Whitney U-test: $Z=-2.270$, $p<0.025$; Fig.

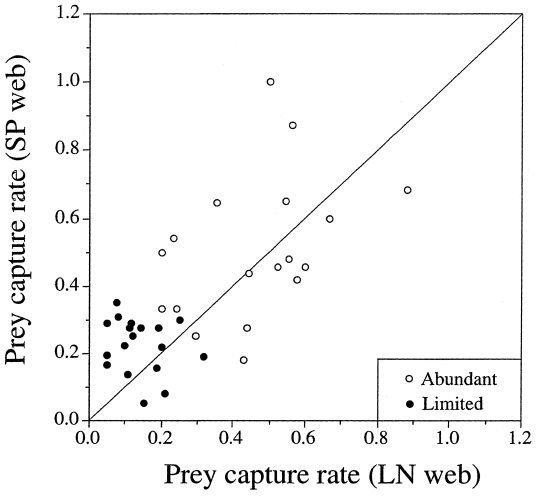


Fig. 5. Comparison of the prey capture rates of the two types of web. The points represent the mean prey capture rates of the two types of web on high (open circles) or low (solid circles) quality days. The daily sample size for each type of web varied from 12 to 16. Under prey-limited conditions, webs with spiral stabilimenta intercepted more prey than webs with linear stabilimenta. Under prey-abundant conditions, there was no significant difference in the prey capture rates of the two types of web.

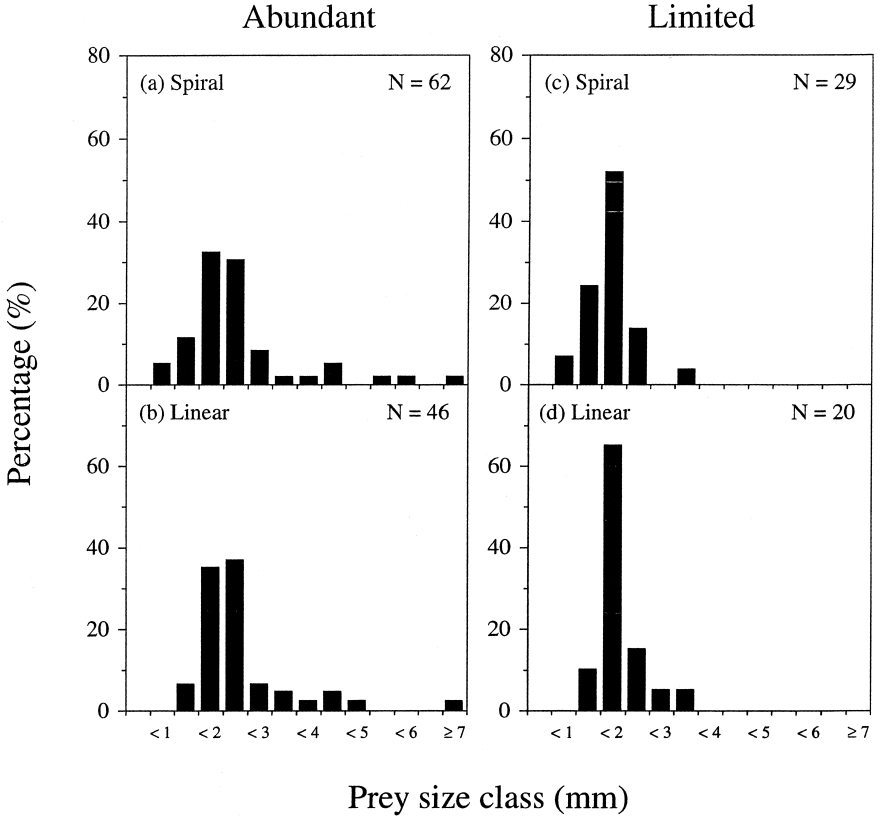


Fig. 6. The distribution of prey size for webs with spiral and linear stabilimenta under abundant and limited prey conditions.

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4). When prey was abundant, the prey capture rate (number of prey per web per census) did not differ significantly between the two web types (SP and LN webs) (Wilcoxon signed-rank test: $Z=-0.805$, $N=19$, $p>0.420$; Fig. 5). In contrast, when prey was limited, the prey capture rate of SP webs was significantly higher than that of LN webs (Wilcoxon signed-rank test: $Z=-2.505$, $N=18$, $p<0.015$; Fig. 5).

The size distribution of prey on spider webs was similar to that on artificial sticky traps; the mode of the frequency distribution occurred at the size range from 1.5 mm to 2.5 mm (Figs. 4, 6a–d). On abundant days, the size of prey captured on SP and LN webs was not significantly different (Mann Whitney U-test: $Z=-1.122$, $N_1=62$, $N_2=46$, $p>0.260$; Figs. 6a, b). On the other hand, the prey captured on the SP webs was significantly smaller than the prey captured on the LN webs when the prey was captured on limited days (Mann Whitney U-test: $Z=-2.32$, $N_1=29$, $N_2=20$, $p<0.020$; Figs. 6c, d). SP webs caught significantly smaller prey under prey-limited conditions than when prey was abundant (Mann Whitney U-test: $Z=-2.564$, $N1 = 62$, $N2 = 29$, $p < 0.015$; Figs. 6a, c), while there was no difference between abundant and limited prey conditions on LN webs (Mann Whitney U-test: $Z=-1.745$, $N_1=46$, $N_2=20$, $p>0.080$; Figs. 6b, d).

DISCUSSION

It seems appropriate to use artificial traps to estimate the potential abundance of *Octonoba sybotides* prey, because the taxonomic composition and size range of the insects captured by webs and traps were similar. In addition, the prey capture rate of the spiders correlated well to the number of insects captured by the traps. The artificial trap caught smaller insects on prey-limited days than on prey-abundant days.

This study demonstrated that under limited prey conditions the orb-webs of *O. sybotides* with spiral stabilimenta (SP webs) caught more prey than those with linear stabilimenta (LN webs), while there was no significant difference in the prey capture rate between SP webs and LN webs under abundant prey conditions. The prey caught by SP webs was smaller than that caught by LN webs under prey-limited conditions. Therefore, the advantage of catching prey in the SP-web seems to be due to a higher efficiency in catching smaller prey.

How can *O. sybotides* catch more prey on a SP web than on a LN web under food-limited conditions? A comparison of the dimensions of the SP and LN webs showed that SP webs have narrower meshes and larger catching areas than LN webs. Therefore, any of the three different web characteristics (stabilimentum form, mesh size, and catching area) might affect the difference in the size distribution of captured prey under prey-limited conditions. The type of stabilimentum might cause a difference in the prey species captured in each type of web. However, there has been no study indicating that smaller dipteran insects are more attracted to UV-reflecting objects with spiral or disc-like forms than to those having linear form. *Drosophila* does not have a preference for stabilimentum form (Watanabe, 1999b), but this possibility cannot be rejected. Catching area seems to directly affect prey-catching efficiency. Although a larger area might increase the number of prey intercepted, it cannot explain the difference in prey size. Mesh size may have a greater effect on the size of prey captured. The size of prey captured by LN webs did not differ between prey-rich and prey-poor environments, although the size of the available prey estimated by artificial traps was smaller under limited-prey conditions than under abundant-prey conditions. This suggests that LN webs with wider meshes are less profitable for catching smaller prey.

An alternative explanation for the difference in the size distribution of captured prey may be a change in the attack behavior of the spider in response to its energetic state. Herberstein *et al*. (1998) examined the effect of foraging history and prey type on the foraging decisions of an orb-web spider, *Argiope keyserlingi*. They found that food-deprived spiders attacked smaller, less profitable flies (*Drosophila*) more frequently than food-satiated spiders, and that food-deprived spiders traveled faster than satiated spiders. Since the speed with which a spider arrives at its struggling prey is critical to capture success, particularly for prey that can escape quickly (Riechert and Łuczak, 1984), food-deprived *O. sybotides* might catch smaller prey. Food-deprived *O. sybotides* responded much faster than satiated spiders to smaller *Drosophila*, while there was no difference in the response speed of spiders under different feeding regimes toward larger *Drosophila* (Watanabe, 2000b). However, webs with a narrower mesh require a greater investment of energy. If the behavioral change alone is sufficient to increase the capture rate of smaller prey, the increased investment cannot be explained. It is likely that food-deprived spiders target a wider range of prey sizes both behaviorally and mechanically. Spiders may improve their prey capture success by increasing their interception of smaller prey, both by constructing webs with a narrower mesh and by responding to prey more quickly.

If a narrower mesh increases the capture efficiency for smaller prey, its results may be negated in a prey-rich environment. There were no differences in the size of prey captured in the two web types. However, the average prey size on SP webs was larger under prey-abundant conditions than under prey-limited conditions. This seemed to be due to an increase in the number of larger prey captured on SP webs under prey-abundant conditions, not to a decrease in smaller prey.

Why don't SP webs, with their larger catching areas, catch more prey than LN webs, under prey-rich conditions? Flying insects may be able to avoid SP webs with their narrower mesh more easily than LN webs, because the narrower mesh makes the web more visible (Craig, 1986; Rypstra, 1982). The catching silks of uloborid spiders have a high UV reflectance (Craig *et al*., 1994). Web visibility may reduce SP webs' rate of prey interception to below that of LN webs, in spite of their larger catching area, especially the interception of larger prey.

The results of this study also imply that spiders in a prey-rich environment should construct LN webs rather than SP

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webs, because LN webs catch equal numbers and sizes of prey with a smaller energetic investment compared to SP webs. In general, web design is not considered to be fine-tuned to specific prey types (Eberhard, 1990). In contrast, this study suggests that *O. sybotides* has the ability to construct two types of web, each of which seems to be suited to the prey availability in their habitat. To date, there is no evidence that *O. sybotides* can assess the abundance of prey in its habitat before prey capture, although some studies have suggested that web-weaving spiders can assess the presence of prey before capturing prey (Morse, 1988; Riechert and Łuczak, 1984). Previous studies showed that the prey capture success of orb-web spiders affects their frequency of web relocation, so foraging success seems to affect their habitat evaluation (Janetos, 1982; Olive, 1982; Vollrath, 1985). A previous experimental study showed that *O. sybotides* constructs SP webs when it is food deprived, while it constructs LN webs when it is satiated (Watanabe, 1999a). Such spiders' rules for choosing a web type may adapt to changes in the environment, since any change in prey abundance in the habitat is reflected in the prey capture rate, and consequently in the spider's energetic state. Actually, a large proportion of spiders add linear stabilimenta to their webs when prey insects are abundant, whereas the majority adds spiral stabilimenta to their webs when prey insects are limited (Watanabe, 2000a). To better understand the foraging strategy of *O. sybotides* with dimorphic web types, relationships between the patterns of fluctuation in resource abundance and the timing of the change of web types must be examined.

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