

Prey Type does not Determine Web Design in Two Orb-Weaving Spiders

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Pavol Prokop (2006) Prey type does not determine web design in two orb-weaving spiders. *Zoological Studies* 45(1): 124-131. Two species of orb-weaving spiders, the diurnal *Argiope bruennichi* and the nocturnal *Larinioides cornutus*, differ in both morphology and time of foraging. I separately investigated the short-term effects of airborne vibrations of prey and prey capture experience on web design and on the likelihood of web building in laboratory conditions. The relationship between web design (especially mesh height) and prey length for both spider species was examined in the field. Neither airborne vibrations nor experience with specific prey affected web design. However, *Larinioides* delayed its web-building behavior in the presence of honeybees which can be considered a novel and/or potentially dangerous prey. *Larinioides* was less successful in attacking honeybees in comparison with *Argiope*, in both laboratory and field conditions. The expected positive relationship between large mesh height and slow-flying, large prey was found in neither the laboratory nor the field. <http://zoolstud.sinica.edu.tw/Journals/45.1/124.pdf>

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Spiders have various foraging strategies which include active pursuit, sit-and-wait, and prey attraction through aggressive mimicry (Uetz 1992). Orb-weavers are sit-and-wait predators who use their webs to catch prey. Once the web is completed, it cannot be quickly or easily modified, so foraging success depends on decisions made before web building. Thus, the quality of the web as a prey trap is the main factor that affects a spider's foraging success (Craig 1989). Designs of webs vary among species and even among individuals of the same species. This variation may be due to differences in leg length (Krink and Vollrath 1999), spatial constraints (Krink and Vollrath 2000), climatic factors (Vollrath et al. 1997), body size (Heiling and Herberstein 1998, Venner et al. 2003), prey capture rates, egg production (Sherman 1994, Herberstein et al. 2000a), prey availability (Pasquet et al. 1994, Herberstein et al. 2000b), or previous experience (Heiling and Herberstein 1999). Furthermore, some studies have documented the effect of prey type on web

design in both the field (Sandoval 1994) and laboratory (Schneider and Vollrath 1998). Sandoval (1994) reported that the orb-web spider, *Parawixia bistriata* (Araneae: Araneidae), constructed either small webs with low mesh height which mostly trapped small dipterans, or large webs with greater mesh height to capture large flying termites. This is consistent with the prediction that webs should have large mesh sizes when prey are large and exhibit low kinetic energy (Sandoval 1994). A significant relationship between prey length and mesh height was also found in other field studies (Murakami 1983, Uetz et al. 1978). On the contrary, several laboratory (Olive 1982, Nentwig 1983) and field studies (e.g., McReynolds and Polis 1987, Herberstein and Elgar 1994, Herberstein and Heiling 1998) did not support this prediction. Recently, Herberstein et al. (2000b) failed to find an effect of prey on web design in the diurnal orb-weaving spider, *Argiope keyserlingi*, under laboratory conditions. Schneider and Vollrath (1998), however, found an effect of prey

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on web design for *Araneus diadematus*. Differences between these study results may involve differences in species biology, or, more simply, differences in methodology or rearing conditions (e.g., not allowing spiders such as *A. keyserlingi* to adjust their web design to the available prey type). The effect of previous exposure to prey types can be very important. A nocturnal spider, for example, has a low probability of encountering diurnal insects that may be offered in a laboratory setting.

The vibrations produced by different prey may provide important information about that prey's profitability (Masters et al. 1986). Recent studies suggest that spiders can distinguish between different kinds of trapped prey. For example, *Nephila clavipes* recognizes unpalatable butterflies and removes them from the web (Vasconcellos-Neto and Lewinsohn 1984). Herberstein et al. (1998) showed that a spider's foraging behaviors vary in response to potential danger posed by the prey, because *Argiope keyserlingi* used different attack behavior toward stinging bees as opposed to non-stinging prey. Olive (1980) also found that *Argiope spiders*, which have longer forelegs than *Araneus spiders*, are more successful in capturing dangerous prey. Thus, spiders may differentially respond to entangled prey that vary in quality.

Airborne vibrations caused by prey significantly affect spiders' foraging decisions in terms of web-building behavior. When prey is present around the spider before web construction, the chance of building a new web increases. On the contrary, the absence of potential prey decreases web-building behavior (Pasquet et al. 1994, Herberstein et al. 2000b). Because the presence of prey provides important information to the spider before building a web, one might predict that the presence of novel and/or dangerous prey would influence web building. To the present time, however, no study has examined the effects of airborne vibrations produced by different types of prey in the context of web-building behavior. The present study investigated the effects of prey type on web design and the likelihood of web building in 2 spider species. I predicted that spiders exposed to prey with high kinetic energy (i.e., heavy, fast-flying insects) would have densely meshed orb webs in contrast to spiders exposed to prey with low kinetic energy (i.e., lighter, more-slowly flying insects). I note that web design may be affected by spider mass regardless of the presence of potential prey. A second prediction is that if the presence of common prey positively affects web-building behavior (e.g., Pasquet et al. 1994), then

the presence of novel and/or dangerous prey should delay web building so as to avoid encounters between the spider and prey. In this study, I studied 2 orb-weaving spiders: the diurnal *Argiope bruennichi* (Scopoli) and the nocturnal *Larinioides cornutus* (Clerck). I tested them using prey-generated airborne vibrations and the spiders' experience with specific prey types on web design. Two types of prey were used: the honeybee and a damselfly. The honeybee, *Apis mellifera*, has high kinetic energy and is a common prey of *Argiope*, but is very rarely captured by *Larinioides* (Kajak 1965, Nyffeler and Breene 1991). These differences stem from different foraging strategies: *Argiope* forages mostly during the daytime, but *Larinioides* usually sits in the web hub during the night. The slow-flying damselfly, *Platynemesis pennipes*, (low kinetic energy) is a common prey item for both spider species (P. Prokop, unpublished data). In contrast to the honeybee, *P. pennipes* poses no danger to these spider species (Herberstein et al. 1998). These differences between the prey species allow for an examination of the effect of novel and/or dangerous prey on the probability of web-building behavior. In addition, if prey length affects web design, then differences in prey body length and kinetic energy should result in differences in web mesh height.

MATERIALS AND METHODS

Laboratory experiment

Adult female spiders of *Larinioides* and *Argiope* were captured in the field from July to Sept. 2003, and were housed in 0.3 L glass containers covered by a fine mesh in the laboratory. They were given water daily, but were starved for 4 d prior to the experiment. On the day of the experiment (day 0), each spider was randomly assigned to one of 3 treatments: damselfly prey (*P. pennipes*), honeybee prey (*A. mellifera*), or a control treatment without prey. Prey species differed in body weight (damselfly, mean weight $\pm$ SE: 0.034 ± 0.002 g, $n = 15$; honeybee: 0.078 ± 0.002 g, $n = 15$), body length (damselfly: 33.60 ± 0.252 mm; honeybee: 14.89 ± 0.193 mm), kinetic energy, potential danger, and/or novelty. The spiders were weighed, and the prosoma width was measured using digital calipers. Each spider was then transferred into a 3-dimensional chamber (40 x 45 x 18 cm). According to the type of treatment, I transferred 3 prey specimens to a small plastic cage (7

x 7 x 7 cm) covered with mesh that was adjacent to the spider's chamber, thereby allowing the spider to detect possible airborne vibrations. No prey was placed in the adjacent chamber of spiders in the control group. On the following day (day 1), I calculated the length of new webs' sticky spirals (capture thread length, CTL) following Venner et al. (2001). The average distance between spirals (ADS) equaled:

$$ADS = \frac{O_v - l_v}{n_s - 2}, \quad (\text{Eq. 1})$$

where O_v is the distance between the outermost vertical spirals, l_v is the distance between the innermost vertical spirals, and n_s is the number of vertical spirals. All spiders that did not built webs were excluded from further experiments. After these web measurements were taken, I removed the cage from the spider's chamber and then introduced a single specimen of the prey type into the chamber. Usually, the prey was captured by the spider and ingested. In some cases ($n = 3$ for *Argiope* and $n = 13$ for *Larinioides* in the honeybee treatment), the introduced prey was first killed and then was placed near the spider's chelicerae which allowed the spider to ingest the prey. This procedure is frequently used in experiments with spiders (A. M. Heiling, pers. comm.). In only 1 case did a spider (*Larinioides*) not ingest the prey, so that spider was excluded from further analysis. After prey ingestion, I broke several lateral radii to collapse the web and encourage rebuilding. This procedure was not carried out with the control treatment, because unfed spiders rebuild webs very rarely after web damage, and there were insufficient samples in the control group.

The next day (day 2), I repeated the web measurements described above, except for the control treatment, because it allowed for comparison of differences between web design before and after the capture of specific prey types. Each spider in the experiment was used only once. All values are given as the mean $\pm$ SE.

Field observations

I conducted field observations to examine possible relationships between prey length and height of the web mesh for adult females of *Larinioides cornutus* and *Argiope bruennichi* in 2 different natural habitats in Slovakia. These species strongly differ in body weight (*Larinioides*: 0.116 ± 0.005 g ($n = 57$) vs. *Argiope*: 0.242 ± 0.013 g ($n = 61$), $t = 8.262$, $df = 116$, $p < 0.001$).

Larinioides cornutus was frequently found in vegetation adjacent to the small river Čierna voda ($48^\circ 21'N$ $17^\circ 39'E$) while *A. bruennichi* was found in a grassland habitat ($49^\circ 28'N$ $19^\circ 23'E$). Both species were observed on several sunny and windless days from June to Aug. (*L. cornutus*) and from July to Sept. (*A. bruennichi*) in 2003. Each web was individually marked using a white ribbon attached to a nearby plant, and surveyed every 30 min from 05:00 until 11:00 in the case of *L. cornutus* and from 06:00 to 12:00 in the case of *A. bruennichi*. All webs of *Larinioides* were intact in the early morning, which indicated that they had been built during the previous night.

The presence of web structures called "stabilimenta" in *A. bruennichi* was not considered in the analyses, because we have found no effect of these structures on web design or on foraging success in this species (Prokop and Grygláková, 2005). I obtained data for 98 *Larinioides* and 41 *Argiope* orb-webs. For each web, I measured the height of the mesh (as in the lab) and the length of the trapped prey from the head to the tip of the abdomen. The prey was either measured directly in the orb-web using digital calipers (*L. cornutus*) or carefully removed from the web, fixed in 8% formaldehyde and later measured under a binocular microscope (*A. bruennichi*). I also noted the presence of honeybees in the orb-webs of both spiders.

RESULTS

Effects of airborne vibrations on web design

In *Larinioides*, the width of the prosoma and body mass significantly differed between the 3 treatments (one-way ANOVA, $p = 0.044$ for both variables). On the contrary, ANOVA showed no differences in prosomal width ($p = 0.57$) or body mass ($p = 0.68$) in *Argiope* between treatments.

Therefore, I used both of these variables as covariates because they affected the web design by adult females (Heiling and Herberstein 1998) and mesh height or capture thread length (CTL) were treated as dependent variables. An ANCOVA showed a significant effect of spider species, but not an effect of treatment on CTL on day 1 (Table 1), whereas *Larinioides* had webs with longer CTLs than did *Argiope* (1203.2 ± 56.3 vs. 832.4 ± 53.8 cm). All of the effects on the height of the mesh were insignificant (Table 1). Both *Larinioides* (2.673 ± 0.735 mm) and *Argiope*

(2.381 ± 0.972 mm) built similarly meshed orb-webs.

Effects of body mass on web design

Larinioides cornutus

After pooling the data and standardizing them for the effect of treatment on day 1, a multiple regression with CTL as the dependent variable showed that both the width of the prosoma and body weight entered the model ($R^2 = 0.149$, $p = 0.013$, $n = 57$), but only prosomal width significantly affected CTL (see Table 2).

I also performed a regression analysis with height of the mesh as the dependent variable, which revealed that both the width of the prosoma and body weight entered the model, but not significantly ($R^2 = 0.095$, $p = 0.066$).

They therefore explained very little of the variation in mesh height (Table 2).

Argiope bruennichi

Using the multiple regression as described for *Larinioides*, the width of the prosoma and body weight both entered the model ($R^2 = 0.163$, $p = 0.006$, $n = 61$), and both significantly affected CTL (Table 3). Similar results were obtained for the

height of the mesh ($R^2 = 0.122$, $p = 0.023$) (Table 2).

Success with the capture of prey

All individuals of both spider species successfully captured the damselfly (day 1). However, only three of 16 *Larinioides* successfully captured the honeybee. In one of these cases, the spider killed the prey out of its orb-web. In contrast, *Argiope* spiders were successful in 20 of 23 attempts on honeybees. This difference was highly significant (Fisher's exact test, $p < 0.0001$).

Effects of capturing the prey

Damselflies

In 13 cases, the damselfly was captured and eaten by *Larinioides*, and the web was rebuilt. I found significant differences between days 1 and 2 in terms of CTL, but not in the height of the mesh (Table 3). A similar, but statistically insignificant, trend was found for *Argiope bruennichi* (Table 3).

Honeybees

In 6 cases, *Larinioides* spiders rebuilt their orb-webs, while in one of these cases, the spider

Table 1. Effects of the type of prey on capture thread length (CTL) and mesh height

Dependent variables	Effect	df effect	df error	F	p
Capture thread length (CTL)	Treatment	2	110	.229	0.795
	Spider species	1	110	4.032	0.047
	Treatment x species	2	110	.311	0.733
Mesh height	Treatment	2	110	.138	0.871
	Spider species	1	110	1.531	0.218
	Treatment x species	2	110	.582	0.561

Table 2. Multiple regression for the effect of body measurements on web measures of females of *Larinioides cornutus* and *Argiope bruennichi*. Beta (β) values and significance are given

Independent variables	Prosomal width		Body weight	
	<i>L. cornutus</i> ($n = 57$)	<i>A. bruennichi</i> ($n = 61$)	<i>L. cornutus</i> ($n = 57$)	<i>A. bruennichi</i> ($n = 61$)
CTL	0.426**	0.381*	-0.13	-0.535**
Mesh height	0.245	0.455**	0.108	-0.368*

CTL, capture thread length; * $p < 0.05$; ** $p < 0.01$.

did not ingest the prey. It is possible that those *Larinioides* fed honeybees were satiated, and this may have reduced their foraging effort. Because the mean body weight of *Larinioides* is only 1/2 that of *Argiope*, a honeybee might represent a greater amount of food to the smaller *Larinioides*. Due to the low sample size, I could not compare differences between webs before and after prey capture.

There were 13 cases in which *Argiope* captured and ingested the honeybee and then rebuilt the orb-web. The CTL significantly decreased, but mesh height did not (Table 4).

Effects of ingesting different prey on web design

For *Argiope*, I failed to detect statistical differences in web design on day 2 between spiders that had captured damselflies and those that had captured honeybees (*t*-test, $p > 0.865$ for all web measures). Because of the small sample size

obtained for honeybees in *Larinioides* (see above), I could not examine the effect of prey ingestion in this species.

Frequency of web building

The probability of web building was slightly affected by prey type. Only 29.63% of *Larinioides* spiders in the honeybee treatment had built their orb-webs by day 1 (Table 5). This difference was nearly significant in comparison with the damselfly and control treatments ($G = 5.17$, $df = 2$, $p = 0.07$). No differences in web-building frequency between the 3 treatments were found for *Argiope* ($G = 1.42$, $df = 2$, $p = 0.49$). Controlling for between-species differences, I standardized the web-building frequencies relative to the average web-building frequency in the control treatments of both species ($36/88 = 0.409$). This value was then used to calculate an index of web-building frequency (i.e., control treatment) of each spider species, i.e. $0.409/(20/47) = 0.96$ for *Larinioides* and

Table 3. Effect of damselfly capture on the web design of *Larinioides cornutus* and *Argiope bruennichi*

Controlled variables	Spider species	Before prey capture	After prey capture	Test statistics	<i>p</i>
CTL (cm)	<i>L. cornutus</i> ($n = 13$)	1270.41 $\pm$ 155.73	991.37 $\pm$ 126.87	$t_{12} = 5.44$	0.001
	<i>A. bruennichi</i> ($n = 17$)	967.85 $\pm$ 108.83	810.34 $\pm$ 108.64	$t_{16} = 1.95$	0.069
Mesh height (mm)	<i>L. cornutus</i> ($n = 13$)	2.73 $\pm$ 1.68	2.53 $\pm$ 1.76	$t_{12} = 1.52$	0.154
	<i>A. bruennichi</i> ($n = 17$)	2.47 $\pm$ 1.67	2.48 $\pm$ 1.63	$z = -0.45$	0.653

Table 4. Effect of honeybee capture on web design of *Argiope bruennichi*

Controlled variables	Before prey capture	After prey capture	Test statistics	<i>p</i>
CTL (cm), $n = 13$	1012.53 $\pm$ 93.12	785.99 $\pm$ 90.78	$t_{12} = 4.482$	0.001
Mesh height (mm), $n = 13$	2.69 $\pm$ 1.68	2.48 $\pm$ 1.87	$t_{12} = 1.785$	0.100

Table 5. Frequency of web building in *Larinioides* and *Argiope*. Spiders were examined for the effects of airborne vibrations (webs built between days 0 and 1) and effects of the prey capture experience (webs built between days 1 and 2). Percentages are given in parentheses

Treatment	From days 0 to 1		From days 1 to 2	
	<i>Larinioides</i>	<i>Argiope</i>	<i>Larinioides</i>	<i>Argiope</i>
Control observed/total	20/47 (42.6)	16/41 (39)	4/20 (20)	3/16 (18.8)
Damselfly observed/total	21/40 (52.5)	22/43 (51.2)	13/21 (61.9)	17/22 (77.3)
Honeybee observed/total	16/54 (29.6)	23/47 (48.9)	6/16 (37.5)	13/23 (56.5)

$0.409/(16/41) = 1.05$ for *Argiope*. I separately multiplied this index by the frequency of web building in the experimental treatments for each species. The standardized web-building frequency in the honeybee treatment was 28.44 (calculated using the residual frequency of 15/54) for *Larinioides* and 51.38 (with a residual frequency of 24/47) for *Argiope*. This difference was significant ($G = 5.79$, $df = 1$, $p = 0.016$). In contrast, no difference between species for the damselfly treatment was found.

Similarly, the frequency of web rebuilding (day 2) for the initial number of spiders used in the honeybee treatment (day 0) was significantly lower for *L. cornutus* (6 of 54; 11%) than for *A. bruennichi* (13 of 47; 28%) (Fisher's exact test, $p = 0.042$).

Field observations

Relationships between web design and prey capture

The average height of the mesh observed in *Larinioides* was 5.09 ± 0.112 mm ($n = 98$). The average length of the prey was 6.27 ± 0.834 mm ($n = 764$). *Argiope* captured longer insects (15.09 ± 0.943 mm, $n = 70$), and built denser webs (with a mean mesh height of 2.20 ± 0.004 mm, $n = 41$). I found no significant correlation between the height of the mesh and prey length in *Argiope* ($r = -0.255$, $p = 0.108$, $n = 41$) or in *Larinioides* ($r = 0.102$, $p = 0.320$, $n = 98$).

Frequency of honeybee capture

Honeybees were found significantly more frequently in the webs of *Argiope* (4 of 41 webs) than in *Larinioides* (0 of 98 webs; Fisher's exact test, $p = 0.007$).

DISCUSSION

This study indicates a lack of short-term responses to airborne vibrations of prey and to prey-capture experience on web design. Web building is costly in terms of the actual production of silk proteins and the movement costs of construction (Eberhard 1986). One could expect a spider to reduce its costs by building stronger (i.e., denser spirals) and smaller webs when the available prey is small with high kinetic energy. Although neither *Argiope* nor *Larinioides* responded to different kinds of prey, it is possible that spi-

ders are less sensitive to short-term changes in prey type, and more responsive to longer-term exposure to prey of specific morphology and behavior (Schneider and Vollrath 1998, but see Olive 1982).

The prey used in this experiment strongly differed in absolute body weight. One could argue that these differences might have affected the results obtained after ingestion due to differences in satiation between treatments. This is unlikely for 2 reasons. First, prey weight as a percentage of spider weight varied only between 14% and 32% (note that data from ingestion of honeybees by *Larinioides* were not used, see "Results" for more details). Second, web design after prey ingestion showed similar trends regardless of prey type.

In both species, the length of the capture threads tended to decrease after prey ingestion. This result most likely reflects the effect of food satiation (Sherman 1994, Tso 1999, Herberstein et al. 2000a, Seah and Li 2002) rather than the effect of experience with different types of prey. In addition, mesh height was not affected by the type of prey.

The frequency of web building and the success of prey capture appeared to be affected by the presence of novel and/or dangerous prey. *Larinioides* was less likely to build a web in the presence of honeybees than in the presence of damselflies. Furthermore, its web-building frequency in the presence of honeybees was significantly lower than that for *Argiope*. These differences could have been caused either by airborne vibrations or by odor cues produced by the prey. Several studies have demonstrated that spiders are capable of detecting odor cues of their predators (Persons et al. 2001, Li and Lee 2004). However, this experiment did not allow for the separation of vibrations and odor stimuli, so the odor hypothesis cannot be ruled out.

The results of this study reflect differences in foraging behaviors between the 2 spider species. In general, diurnal spiders remain in their webs throughout the day and night, while nocturnal ones spin their webs at dusk and ingest their webs at dawn (Stowe 1986, Herberstein and Elgar 1994). Unlike *Argiope*, *Larinioides* builds its web in the evening (Sherman 1994), and it is classified as a nocturnal spider (sensu Nyffeler and Benz 1989), although its orb-webs remain exposed during the day. Adult *Larinioides* females only rarely are present in the web hub during the day (P. Prokop, unpublished data). On the contrary, *Argiope*

rebuilds its web in the early morning and actively catches prey during the day. Thus, differences between diurnal and nocturnal activities reflect the spiders' presence in the web hub, but other details about prey capture success of "nocturnal" *Larinioides* and "diurnal" *Argiope* remain unclear.

Considering morphology, *Argiope*, with its longer 4th (wrapping) legs, is able to capture more-dangerous prey than is either *Araneus* or *Larinioides* (Olive 1980). Because *Larinioides* is active mostly at night, the probability of capturing honeybees is low. This suggestion is supported by the present study and published field observations that show that honeybees are only rarely caught by *Larinioides* (Kajak 1965, Nyffeler and Breene 1991). In contrast, Nyffeler and Breene (1991) found that honeybees comprised 15% of prey specimens collected from webs of *Argiope*. During field observations, I also noted a significantly higher frequency of honeybees in *Argiope* webs than in *Larinioides* webs. Moreover, I observed that most individuals of *Larinioides*, unlike those of *Argiope*, were significantly less likely to catch honeybees, despite actively responding to their presence in the web. In this scenario, airborne vibrations originating from unprofitable prey can convey important information to spiders about prey identity.

Effects of morphology on web design, especially on mesh height, are interesting in light of mixed results from other studies (see Heiling and Herberstein 1998 and references therein). In the present study, the effects of body size measures on web design were strongly species-specific. Capture thread length of both species was significantly affected by prosomal width (see also Olive 1980, Murakami 1983). On the other hand, despite a correlation between prosomal width and body weight, their effects on capture threads differed. This negative relationship between body weight and CTL was clearly significant for *Argiope*, with *Larinioides* showing a similar trend. This is not surprising, because heavier spiders must devote more energy to web building (Venner et al. 2003) and cocoon production, so their foraging investment in web production should be lower (Sherman 1994). An opposite relationship was found for *Larinioides sclopetarius* (Heiling and Herberstein 1998). Interestingly, mesh height variation in *Argiope*, but not in *Larinioides*, was likely a function of morphological specializations rather than a response to specific prey.

Prey capture can differ strongly between nocturnal and diurnal spiders. Nocturnal spiders may predominantly catch moths, whereas diurnal spi-

ders may mostly catch Hymenoptera (Herberstein and Elgar 1994). Interestingly, orb-webs of *Larinioides* were all found to be intact in the early morning without indications of previous prey capture, such as tracks left by prey (Craig 1989). It is unclear if these webs were simply unsuccessful during night foraging, or if they were built in the early morning. By mid-morning, most of the *Larinioides* orb-webs had trapped prey, so it seems that diurnal foraging is also important for *Larinioides*. Perhaps it is possible that *Larinioides* employs both nocturnal and diurnal foraging tactics. This question warrants future research.

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