

SIGNAL POLYMORPHISM IN THE WEB-DECORATING SPIDER *ARGIOPE ARGENTATA* IS CORRELATED WITH REDUCED SURVIVORSHIP AND THE PRESENCE OF STINGLESS BEES, ITS PRIMARY PREY

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Abstract.—Many spiders, and in particular those in the genus *Argiope*, spin highly visible web decorations whose function and significance are the subject of spirited debate. In this work, we present data to address two of the competing hypotheses that fuel this controversy. In particular, we examine the relationship between the presence of web decorations and spider survivorship (predator-protection hypothesis) and the relationship between the presence of prey and spider decorating behavior (the prey-attraction hypothesis). Our laboratory studies reveal that the decorating behavior of the spider *A. argentata* has a genetic component but that the expression of decorating behavior tends to be elicited only when a spider is well fed. Furthermore, our field studies show that in the presence of abundant stingless bees, spider decorating behavior is induced. Nevertheless, our field surveys also suggest that spiders that decorate their webs show reduced survivorship. We propose that the high correlation between web decorating in the presence of stingless bees supports the hypothesis that *A. argentata* engage in decorating behavior when attracting or targeting specific prey types. However, we also propose that web decorations attract the predators of *A. argentata* because high-frequency decorators suffer lower survivorship than spiders that decorate moderately or rarely. These findings suggest that spider web decorating behavior is affected by conflicting selection pressures: the positive effect of prey attraction versus the negative effect of predator attraction. Due to the heritable component of decorating behavior, web decorating among *A. argentata* is likely to be particularly sensitive to the spider's local ecology as well as local patterns of gene flow.

Key words.—Bees, lineage effects, pollinator, polymorphism, spider, survivorship, web decoration.

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The operating principle of all animal visual systems is to detect contrast. This includes contrasting patterns, orientations, object sizes, height differences, distances, brightness, and colors. Colors and patterns that evolve in animal defense result either in crypsis (contrast minimization) and reduced visibility or aposomatism (contrast maximization) and enhanced visibility that advertises a defense worth avoiding (Endler 1988). Almost all analyses of the function of color and pattern in predator-prey interactions have been viewed from the perspective of mobile, vertebrate predators (Sullen-Tullberg 1985). When an animal is both aposomatic and stationary, however, it is important to weigh the effects of color and pattern from the perspectives of both the animal's predators as well as its prey (Paulson 1973; Craig and Ebert 1994).

One example of a group of predators subjected to conflicting selection pressures is the aerial web-spinning spiders in the genus *Argiope*. *Argiope* species are characterized by diverse body colors and patterns that are sometimes cryptic (repeating lines of black, yellow, and silver conceal *A. trifasciata* against background vegetation) and sometimes aposomatic (mosaic of yellow and black make the coexisting spider, *A. aurantia*, appear wasplike). All *Argiope* species, however, decorate their webs with highly visible, ultraviolet (UV) reflecting, silk patterns that contrast with the web's background vegetation (Craig and Bernard 1990) even when the spiders' color and pattern do not.

Web decorating is unique to the orb-spinning spiders (Orbicularae: Deinopoidea, Araneoidea). Orb webs built by the

Araneoidea are spun from silk that is characterized by both high strength and high extensibility. Insects are intercepted because webs are able to absorb insect impact energy (e.g., Denny 1976; Craig 1987a). Most web silks spun by the araneoids are refractive and from most angles reflect very little light, making them difficult to see. However, a taxonomically diverse array of orb spinners have evolved to decorate their webs with crosses, spirals, or tufts of bright-white, UV-reflecting silk despite the cryptic nature of the orb web (Fig. 1). A phylogenetic analysis of decoration patterns and the taxa in which they occur shows that web-decorating behavior has evolved independently several times (Scharff and Codrington 1997) as have the decorative patterns that the spiders spin (Herberstein et al. 2000a).

Several hypotheses have been generated regarding the function of web decorations. The hypothesis that web decorations serve to attract prey has been most strongly supported by experimental and correlative studies in the field and laboratory (Craig and Bernard 1990; Tso 1996; Hauber 1998; but see Blackledge and Wenzel 2000). However, if decorated webs always attract prey, all spiders should decorate their webs daily, but the majority of web spinners do not decorate their webs (Herberstein et al. 2000a). Furthermore, even conspecific web decorators that forage side by side show variable web decorating behaviors (Craig 1994). This may suggest that spider web-decorating behavior has a genetic component and that it is particularly sensitive to the ecological environment in which the spider is found.

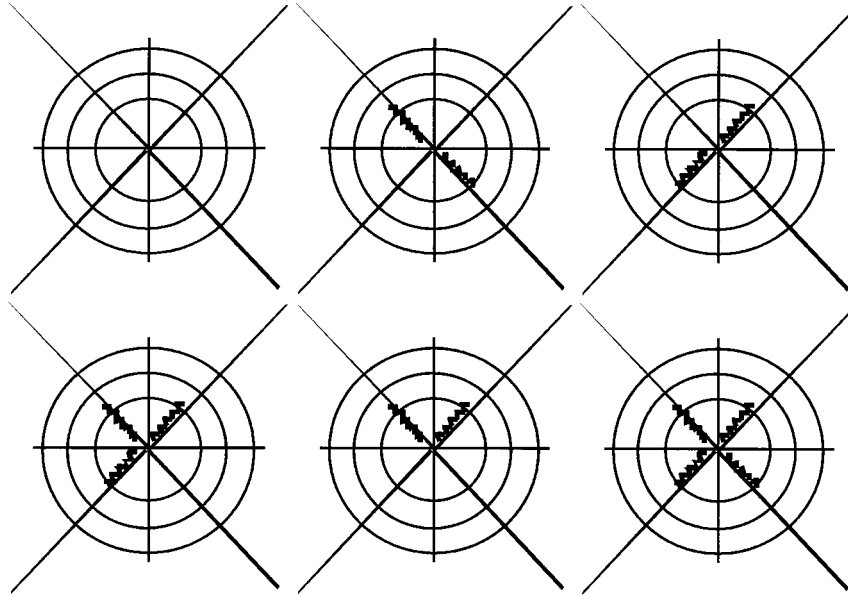


FIG. 1. A sample of patterns of web decorations spun by the spider *Argiope argentata*. Among adult *A. argentata* found on Barro Colorado Island, we observed 16 different types of web decorations composed of one to four arms of a cross. In most cases, arms of the cross were oriented so that they lay in the positions of 2, 5, 7, and 10, as would be viewed on the face of a clock.

Bees are able to recognize patterns on the basis of pattern orientation alone (Hateren et al. 1990). Therefore, one cost of web decorating may be the ability of some insects to learn to avoid webs that are decorated the same way each day (Craig 1994; Blackledge 1998a). This hypothesis was tested via experimental studies with the spider *A. argentata* and one of its most important prey, *Trigona fucipennis*. The experiments showed that stingless bees learned to avoid spider webs that were decorated the same way day after day. Avoidance learning was slowed or inhibited, however, if the orientation of the decoration was varied (Craig 1994). However, if bees can use decorations to avoid webs, then predatory wasps that share similar visual systems and learning behavior may be able to use web decorations to locate spider web sites as well (Robinson and Robinson 1978; Hauber 1999). For example, sphecid wasps are the only documented predators of *Argiope* (Muma and Jeffers 1945; Krombein et al. 1979) and one of us (C. L. Craig) observed two different instances when a large wasp landed on the cephalothorax of an *A. argentata* and stung it. In both cases, the wasps remained in the web area until the spiders had moved off the web and became paralyzed. The wasps then carried the spiders away from the web area, presumably to fortify their nests.

We report the results of experimental tests of some of the possible ecological and behavioral factors that can influence the evolution of web decorating among the orb-spinning spiders, and, in particular, among spiders in the genus *Argiope*. To facilitate experiments isolating possible selective factors, we maintained a laboratory population of *A. argentata*, a large, orb-spinning spider that is normally distributed throughout the American tropics and subtropics (Levi 1968). First, we conducted a series of breeding experiments to determine if different decorating behaviors are inherited. We then explored the effect of food availability on spider decorating behavior by sampling paired offspring from the same

egg sac and randomly assigning them to one of two experimental groups. The two groups of spiders were maintained different diet regimes: one group was maintained on a high-input diet and the other on a low-input diet. The decorating behavior of all of the spiders was recorded.

To determine if spiders varied their decorating behavior under natural conditions, we tracked individually marked, freely foraging spiders. During a first field season and the first half of a second season, the spiders were observed relatively undisturbed in their natural habitat of mixed grasses. During the second half of the second season, however, we manipulated the presence of bee populations by cutting the field completely. Subsequently, spiders were tracked to determine if their decorating behavior correlated with the regeneration and flowering of grasses in the field and the fluctuating abundance of stingless bees. Finally, we combined our data from both field seasons to determine if there was a relationship between decorating behavior and spider survivorship.

METHODS

Pedigree Analysis

A population of approximately 30 *A. argentata* (Fabricius) were collected from Miller Clearing on Barro Colorado Island, Smithsonian Tropical Research Institute, Republic of Panama. The spiders, collected in August (middle of the rainy season) when they are abundant, were transported to an environmental chamber. The environmental chamber was maintained at physical conditions similar to those in the spiders' natural habitat during the rainy season and when these spiders are most abundant. The climate on Barro Colorado Island is seasonal and the forest vegetation is classified as tropical moist forest (Holdridge System). The average temperature is 26°C with an average diurnal range of 8°C and high humidity

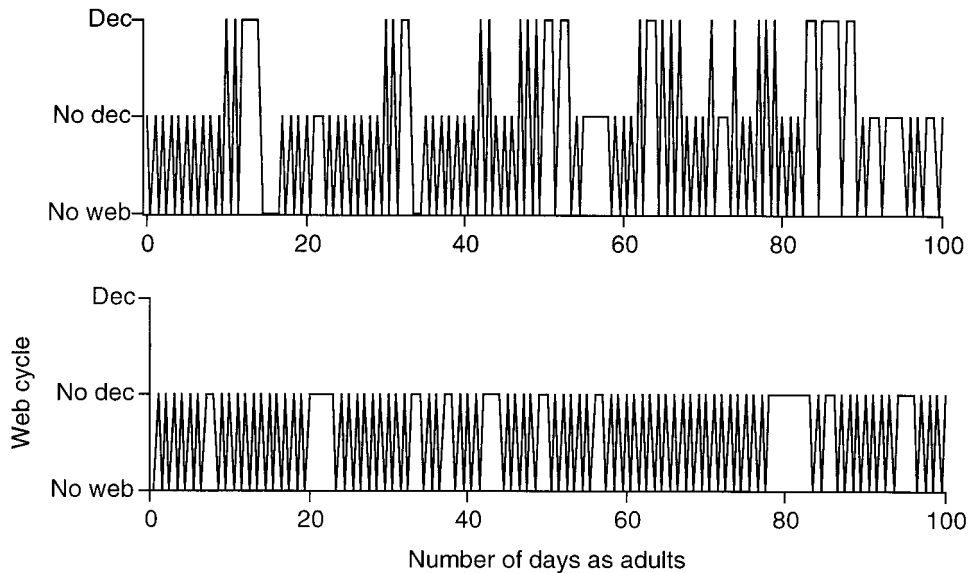


FIG. 2. Individual spiders display variable decorating behavior. We monitored the decorating behavior of a laboratory population of adult *Argiope argentata* while they were maintained on a constant diet of crickets. The data illustrate the web-spinning and web-decorating behavior of two spiders spun over a 100-day period. Each fluctuation in the traces indicates one web cycle. Spiders spun new webs but did not decorate them (a spike to the "No dec" position on the y-axis); they took down their webs (trace returns to "No web" position on the y-axis); they retained the web for two or more days (trace lies parallel to the x-axis) or they spun a decorated web (spike to "Dec" position on the y-axis). Thus, the graphs allow the decorating behavior of individual *Argiope* to be easily quantified and compared.

(<http://www.si.edu/organiza/centers/stri/evsir1.htm>). The environmental chamber where several generations of *A. argentata* were raised was maintained under a constant light cycle (12:12 L:D), at constant temperature (26°C) and constant humidity (80–90%). In addition, by an appropriate choice of lamps and filters, the spectral content of light in the chamber was matched to the spectral content of light in the sites where the spiders foraged. The lamps in the control chamber were wired into three banks, each powered by a separate leg of a three-phase circuit, to decrease the magnitude of the light pulsations and to push their frequency beyond the flicker-fusion frequency of the visual systems of the insect eye (Shields 1989).

The spiders were maintained on a constant feeding regime. When the spiders were adults, their behavior varied between decorating their webs in spurts and at seemingly random intervals to a complete absence of decorating behavior (Fig. 2). To determine the probability that a decorating phenotype might have a genetic component, females of known decorating behavior were crossed with males classified by the decorating behavior of their mothers. The egg sacs of the crossed females were collected and placed in ventilated, Plexiglas boxes for rearing. All spiderlings were identified with numbered tags starting at their third to fourth stadia and the tags were replaced after each molt. The crosses yielded 52 offspring whose lifetime decorating behaviors could be recorded. These data were especially difficult to collect because three to four times as many spiders had to be monitored to obtain the lifetime records of spider decorating behavior that we could include in the final analysis.

Response to Variable Food Resources

To determine if decorating behavior is expressed in response to food availability, we selected paired offspring from

adult females. The spiders included in this experiment were those whose mother's phenotype and father's maternal phenotype had been recorded. We attempted to control for any potential genetic effects by randomly assigning one spiderling from each offspring pair to the high- or low-food treatment groups. The numbers of offspring from each behavioral category, however, could not be balanced due to the difficulty of obtaining parents and offspring whose lifetime decorating behavior was known.

Thirty-five pairs of sibling spiders that had either reached the penultimate stadia or that were sexually mature were selected. Each pair was then split and one individual was randomly assigned to each of the two groups. Spiders in one group were fed one cricket daily, whereas spiders in the second group were fed one cricket every third day. To make sure that the food was available, crickets were individually placed in each web. The next day we recorded whether the spider had fed on the insect or ignored it.

Correlation among Decorating Behavior, Prey Abundance, and Spider Survival

The field site, a 200 × 50 m mixed shrub and grass field, was defined and isolated by surrounding forest on three sides and the Panama Canal on the fourth. In a previous study (unpubl. data), we marked and tracked both adult and juvenile *A. argentata* that were found in a 50 × 100 m area of the field. Although individual spiders changed web sites during the study, they moved only short distances and rarely more than 3–5 m at a time. Thus, relocating the spiders was relatively easy. If a spider could not be found, we searched around the site for at least three days after it had disappeared, as well as throughout the rest of the study area. On the basis of our mapping experiment and search procedures, as well

as the fact that the field was delineated by unsuitable habitat on four sides, we feel confident that the spiders that we recorded as disappeared had, indeed, been preyed upon.

Between June and August 1993, 52 adult or subadult, individually marked spiders were monitored for a minimum of 10 days and a maximum of 43 days. Webs and spiders were surveyed once each hour for an average of five hours daily. Data on web size, the presence or absence of decorations and captured prey were collected. At the end of each daily observation period, spiders were fed one cricket to substitute for prey collected by the observers.

During the 1994 field season, 93 individually marked, freely foraging spiders were surveyed between July and December for a minimum of 10 days and a maximum of 49 days. We recorded the spiders' locations and the decorations, if any, that they spun. Due to the large number of spiders observed each day, we were unable to record rates of prey capture throughout their feeding period. Instead, we focussed on recording the presence or absence of the spiders' most important prey, stingless bees (Craig and Ebert 1994). At the same time each day, we walked a linear, 150-m transect down the center of the site and counted the number of stingless bees that could be sighted within 2 m of the transect line.

Two months into the second season, the site was completely cut, effectively resetting the growth cycle of the grasses to early rainy season conditions. During this time, surviving adult spiders moved to the edges of the field to feed and very small offspring could be found in nongrass areas of limited vegetation that had not been cut. Approximately 30 days after the cut, when grasses had grown tall enough to allow web suspension, we returned to the field and continued our census regime. We recorded the decorating behavior of the few spiders that survived the cut and that of newly found penultimate or adult spiders. In addition, we sampled the number of stingless bees found in the field during the period of grass regeneration through grass flowering. We do not know the effect of the cut on the wasps that preyed on the spiders. We do know, however, that the wasps we observed were subterranean nesters. We suspect that the cut had little effect on their burrows but may have extended the wasp's foraging range.

The Kaplan-Meier method of survival analysis was undertaken to determine if spiders that decorated webs at high, medium, and low frequencies were characterized by different survival rates (SAS Institute 1995). This method of univariate analysis estimates survival rates for one or more groups of right-censored data (i.e., data including spiders that were alive when the experiment ended). The data were further analyzed using two statistical tests. The log-rank test places more weight on longer survival times and is most useful when the death rates at any given time are approximately constant, whereas a Wilcoxon test places more weight on early survival times and is the optimum rank test when the error rate is logistic.

RESULTS

Pedigree Analysis

Analysis of the behavior of 156 spiderlings revealed a common developmental shift in decorating phenotype that

TABLE 1. Pedigree data for web-decorating behavior of adult female offspring. Males are classified by the decorating behavior of known mothers. All females were mated with just one male, although multiple offspring may be from one or more eggs sacs. The number of decorated webs spun by of each of the offspring was normalized, and the spiders were classified into three groups: (1) spiders that decorated their webs rarely or not at all (L; < 25% of all new webs decorated); (2) spiders that decorated their webs with moderate frequency (M; 25–75% of all new webs decorated); and (3) spiders that decorated their webs with high frequency (H; > 75–100% of all new webs).

Female ID	Female decorating frequency (%)	Male decorating frequency (%)	Offspring decorating frequency
Females that decorate at high frequency × males whose mothers decorate at medium frequency			
AB98	96	45	H
Females that decorate at high frequency × males whose mothers decorate at low frequency			
AR50	96	4	L, M, M, M
AB22	91	0	L, M, H
AG67	89	5	L
AG37	81	5	L
AB1	80	5	L, L, L
Females that decorate at medium frequency × males whose mothers decorate at high frequency			
AG2	65	89	M, L
Females that decorate at medium frequency × males whose mothers decorate at low frequency			
AG99	52	25	L, L, L, L, M
AW83	65	6	L, L, L, L, L
Females that decorate at low frequency × males whose mothers decorated at high frequency			
AY91	0	89	L, L, H
Females that decorate at low frequency × males whose mothers decorated at medium frequency			
AY44	0	52	M
Females that decorate at low frequency × males whose mothers decorated at low frequency			
AW76	0	0	L, L, M, M
AR59	0	0	L, L, L
AG87	0	0	L, L, L
AY36	24	25	M, L, L
AY77	19	0	L, L, L, L, L
AR56	19	0	L
AG46	0	0	L, L

occurred at about the fifth molt. Prior to the fifth molt, most spiders decorated their webs daily; after the fifth molt, spider decorating behavior changed radically and in all cases its frequency dropped. To make sure that the behavior of juvenile spiders did not bias the behavior recorded for adults, all of our calculations are based on the decorating behavior of females only after they had reached sexual maturity.

The web-decorating behavior of the spiders for which the web decorating behavior of the parents was known is presented in Table 1. We calculated the regression coefficient of the mean phenotypic behavior (the ratio decorated webs/total webs) of the parents (for male decorating behavior we used the decorating mother of the male's mother) versus that of their offspring to obtain a population estimate of realized heritability (Hartl 1988). The index, h^2 , was significant ($h^2 = 0.26$; $r^2 = 0.11$, $F = 6.1$, $df = 51$, $P = 0.02$). The data

indicate that decorating behavior is affected by the behavior of both the male and female parents and that it has a genetic component. Nevertheless, it is important to emphasize that the calculated index is a population-specific estimate. Furthermore, the spiders included in the experiment were based on those available, thus the experimental group could not be balanced for all of the phenotypes we observed.

Response to Available Food

Although the spiders showed significant, individual variation in their decorating behavior as would be predicted if there was a genetic component to their phenotype (Type I SS, $F = 133$, $df = 34$, $P < 0.0001$), as experimental groups, the spiders responded significantly differently to the food regimes. Spiders maintained on a high prey diet decorated 20% of all new webs; spiders maintained on a low prey diet decorated only 11% of all new webs (ANOVA for whole model: $n = 35$, $r^2 = 0.74$, $F = 144$, $df = 2$, $P < 0.0001$; effect of food regimes, Type I SS, $F = 529$, $df = 2$, $P < 0.0001$). Herberstein et al. (2000b) found a similar response pattern for the closely related spider *A. keyserlingi*, but they also demonstrated that spider behavior varied depending on whether prey were received on a predictable or random schedule. Both of these studies, done in the laboratory, show that decorating behavior can be induced in spiders that are maintained on a high-input diet.

Correlating Decorating Behavior, Stingless Bee Abundance, and Spider Survival

Throughout the 1993 field season, the spiders were relatively undisturbed and observed daily to determine the rates at which they decorated their webs and whether the presence of web decorations correlated with rate of prey capture. An ANOVA ($r^2 = 0.44$, total number of observations = 1100, $F = 6.8$, $df = 114$, $P < 0.0001$) demonstrated that although prey capture rates varied temporally (number of days = 47, $F = 13$, $df = 47$, $P < 0.0001$), spatially (number of field locations = 12, $F = 3.6$, $df = 10$, $P < 0.001$), and at individual web sites (number of sites, $n = 54$, $F = 1.4$, $df = 53$, $P = 0.03$), there was no suggestion of a decoration effect (decoration presence or absence, $n = 2$, $F = 2.3$, $df = 1$, $P = 0.11$). At first glance, these results seem to conflict with experiments done at the same site on *A. argentata* during previous years, which showed that decorated webs intercepted more pollinators than webs that were not decorated (Craig 1991; Craig and Freeman 1991). The difference between these observations, however, can be attributed to the fact that the earlier studies were experimental and the decorations that the spiders spun were manipulated and balanced by site. The data presented here are simply observational. Statistical analyses of three previous studies show that the extreme spatial and temporal variability that characterizes the web sites *A. argentata* on Barro Colorado Island (Craig and Bernard 1990; Craig 1991; Craig and Ebert 1994) will mask the effect of the presence or absence of web decorations the rate of prey interception.

Nevertheless, when the field was completely cut, ANOVA of data gathered during the pre-cut and post-cut periods of the 1994 field season showed that the decorating behavior of the

spiders differed significantly between the two periods (whole model, $r^2 = 0.6$, $n = 65$, $P < 0.0001$; effects, Type I SS, $P < 0.0001$). In fact, during the first half of the season, decorating behavior and the presence of bees appears to vary inversely (Fig. 3a, b). After the field was cut and during regeneration, however, decorating behavior correlated with the flowering of the grasses and the subsequent increase of bees in the field (whole model, $r = 0.34$; effects, Type I SS, $P < 0.02$; Fig. 3c, d).

The Kaplan-Meier method for survivorship analysis showed that the mean lifetimes of spiders that decorated their webs at high (lifetime $\bar{x} = 12.6$ days, $SD = 1.67$, $n = 14$), medium (lifetime $\bar{x} = 20.6$ days, $SD = 1.6$, $n = 58$), and low frequencies (lifetime $\bar{x} = 16.6$ days, $SD = 0.62$, $n = 183$) were significantly different (Wilcoxon $\chi^2 = 7.0$, $P = 0.03$; log-rank $\chi^2 = 8.8$, $P < 0.01$; Fig. 4). Spiders that decorated their webs at the lowest frequency and who are likely to be the least successful foragers lived an average four days longer than spiders that decorated their webs at the highest frequencies and who were likely to be the most successful foragers (Craig and Bernard 1990; Craig 1991; Craig and Ebert 1994). In contrast, spiders that varied their decorating behavior lived eight days longer than spiders that decorated frequently and four days longer than spiders that decorated only rarely.

DISCUSSION

The functional hypotheses of web decorations and the evidence supporting them have been reviewed in detail by Herberstein et al. (2000a). In summary, they include: (1) stabilizing and strengthening the web (Robinson and Robinson 1978); (2) hiding and concealing the spider from predators (Edmunds 1986; Schoener and Spiller 1992; Blackledge 1998a); (3) advertising the web to large animals, such as birds, who might otherwise damage it (Eisner and Nowicki 1983); (4) attracting prey to the web (Craig and Bernard 1990; Craig 1991; Craig and Ebert 1994; Tso 1996; Hauber 1998); (5) promoting thermoregulation (Humphries 1992); (6) regulating silk production (Peters 1987); and (7) reflecting some type of physiological stress (Nentwig and Rogg 1988). Hypotheses 1–6 predict that decorating behavior lends spiders a quantifiable advantage over nondecorators and thus in all cases would result from positive selection. However, among the hypotheses that have been subjected to careful experiments, only the prey-attraction hypothesis has been tested and supported both in the field and laboratory. In both cases the experimental results revealed a web-decorating advantage.

Hypotheses 2 and 3 suggest that decorations advertise webs and thereby prevent large animals from flying into them (Eisner and Nowicki 1983; Blackledge 1998b), decorations enhance spider size and discourage predators from trying to consume them (Schoener and Spiller 1992), or decorations hide the spiders altogether (Eberhard 1973). Our field data showed the opposite effect, that is, high-frequency web decorators have, in fact, reduced survival. The spiders that decorated their webs at the lowest frequency had the next lowest survival rate, and spiders that decorate their webs at moderate frequencies survive the longest.

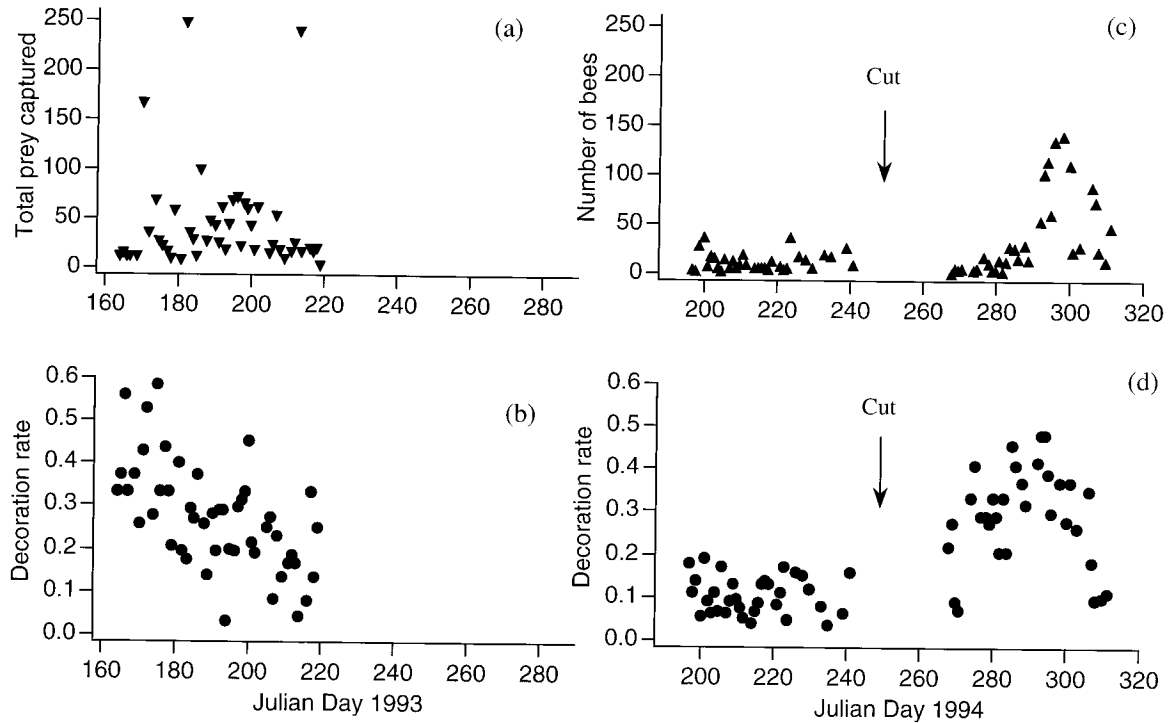


FIG. 3. Comparison of the proportion of decorated webs per day and the total number bees captured per day (in 1993; a, b). The number of bees sampled in the field each day and the proportion of spider that decorated their webs (in 1994; c, d) for both the pre- and postcut periods. Panels (a, b) indicate no clear relationship between web decorating and the number of bees collected from the spiders' webs. Panels (c, d) show spider decorating is correlated with the presence of prey. During the pre-cut period, the decorating behavior of spiders and the presence of bees appears to vary inversely. During the postcut period, however, the decorating behavior of the spiders is entrained with the flowering of the grasses and the increase in the abundance of bees at the study site.

The prey-attraction hypotheses does not directly address spider survivorship, although its underlying assumption is that web decorators that attract prey will grow faster and show a reproductive advantage over nondecorators. Prey intake among spiders has been correlated with reproductive output (Wise 1979; Miyashita 1990, 1992) and high rates of prey input result in faster growth and early maturation (Craig 1987b). For organisms that exhibit low fecundity (in the case of spiders, 150 or fewer eggs per clutch), Lewontin (1965) calculated that a three-day reduction in time to first reproduction has the same impact on a population's intrinsic rate of increase as does doubling the fecundity per individual. This effect should be particularly important to orb spinners because their rate of egg production has been shown to be the most variable factor affecting spider reproductive performance (Eberhard 1979).

Some investigators argue that if prey are plentiful, web enhancements are not necessary. We suggest that web decorations spun by *A. argentata* attract a specific group of prey, stingless bees, and are only spun after the spider has met its minimum energetic needs. This work is supported by Hauber's (1998) observations that demonstrated that decorated webs spun by *A. appensa* were significantly smaller than undecorated webs; the same result was also found for *A. argentata* (unpubl. data) and *A. keyserlingi* (Herberstein et al. 2000b). Other investigators argue that decorating behavior could reflect some type of physiological stress. This argument is not supported by our laboratory studies, which showed that

when a large breeding population of *A. argentata* was maintained under constant environmental conditions and feeding regime, there are always some spiders that decorate their webs and others that do not. Furthermore, if spiders are stressed due to reduced food availability, decorating behavior will be suppressed, not initiated. We did not quantify survival rates of phenotypes under controlled conditions and cannot determine if decorators wear-out sooner than spiders that do not decorate their webs. The fact that decorating *A. argentata* tend to spin smaller webs than nondecorating spiders, however, does suggest that the relative energies expended in each of the web types may be balanced in some way.

We tested the prediction that web decorations could serve a protective function by combining all of our field data for 1993 and 1994 and assessing spider survivorship. The spiders were divided into the high-, medium-, and low-frequency decorating groups that had been suggested by our previous pedigree analysis (done in the absence of predators and while the spiders were maintained on a constant food and environmental conditions). The field data show that only seven of 255 spiders (3%) survived more than 10 days if they decorated their webs at high frequency. These results are inconsistent with the predator-protection hypothesis, but support the hypothesis that the conspicuous web decorations spun by *A. argentata* may actually attract predators of the spiders, thus making them more vulnerable to predation (Robinson and Robinson 1978). Furthermore, when viewed in light of the prey-attraction hypothesis, the data suggest that the con-

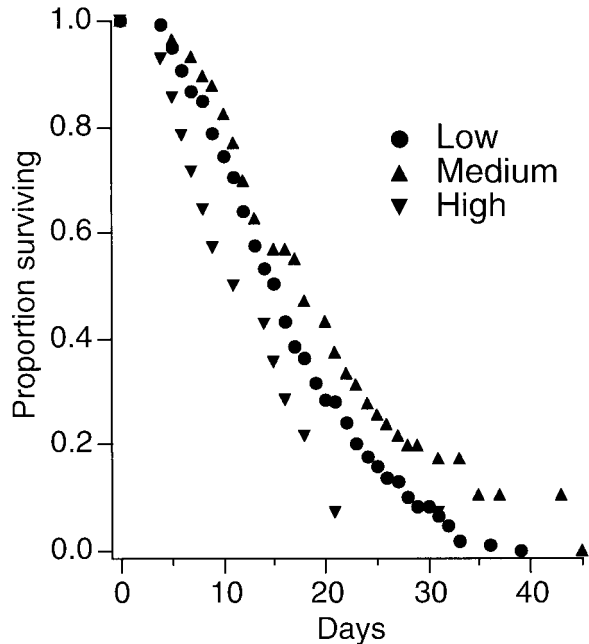


FIG. 4. Survivorship among freely foraging spiders varies among those grouped as low- (< 25% of all new webs were decorated), medium- (25–75% of all new webs were decorated), and high-frequency decorators (> 75–100% of all new webs). Our field data reveal that spiders decorating 75% or more of their webs suffer significantly reduced survivorship. Therefore, although web decorations attract prey, they seem to attract the spider's predators as well.

flicting effects of reduced survivorship versus foraging success favor the retention of decorating polymorphism within populations, as well as variability in individual decorating response. We propose that the prey-attraction hypothesis be revised to a more general hypothesis of insect attraction.

None of the previous seven hypotheses address the possibility that web-decorating behavior is inherited. We found that the decorating behavior of *A. argentata* has a genetic component and that the expression of web-decorating behavior is subject to local ecological conditions, in particular, the presence of prey.

In summary, our results do not support the predator-protection hypothesis or the web-protection hypothesis, and they do not address the web-stabilization, thermoregulation, or silk-regulation hypotheses. They do support the hypotheses of prey attraction (particularly bees), predator attraction, and the idea that decorations reflect spider physiological state. Furthermore, our data predict the testable hypothesis that spiders who carry a high-decorating phenotype and forage in favorable environments will grow faster and reach reproduction sooner than spiders that do not. Finally, the seemingly lineage-dependent yet ecologically induced expression of web-decorating behavior and the high cost of web decorating but high reproductive payback when a decorator gets lucky make the evolution of this behavior particularly sensitive to local ecological conditions.

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