Micronesica 2013-07: 1–15

Predator exposure and size-related variation in web-building and web-decorating behavior in *Argiope appensa*[1]

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Abstract—The spider, *Argiope appensa*, is one of the most abundant and widely distributed species in the Marianas archipelago. Spiders of the genus *Argiope* build conspicuous silk decorations which have been hypothesized to function as visual signals that attract prey, deter predators, or warn oncoming birds of the web's presence to prevent inadvertent damage. Here, we set out to test the hypothesis that spiders will build smaller webs and larger, more complex web decorations in response to the presence of birds. The neighboring islands of Guam and Rota in the Mariana archipelago represent a unique situation to test this hypothesis in a large-scale natural setting. Guam has lost majority of its native avian fauna in the last 50 years as a result of an introduced predator, while other islands in the Mariana archipelago, including Rota, still possess intact native bird populations. We surveyed forest edges on Guam and Rota to assess the influence of two factors – extrinsic (predator exposure) and intrinsic (spider body size, i.e., age) – on web size, web decoration length, and decoration pattern. Web size, web decoration length, and web decoration pattern were correlated with the body size of spiders (ontogenic stage). Web size and web decoration length increased with body size and only smaller (younger) spiders built decorations with cruciate patterns. Exposure to birds did not result in a significant variation in webs size and web decoration between islands. Nevertheless, Guam spiders are trending towards building larger webs

[1] Citation: Raymundo, M.L.H. & C.F. Caballes. 2013. Predator exposure and size-related variation in web-building and web-decorating behavior in *Argiope appensa*. *Micronesica* 2013-07, 15 pp. Published online 23 Dec. 2013. www.uog.edu/up/micronesica/2013.

and shorter web decorations. The diagonal web decoration was the most dominant pattern in both islands, but the frequency of webs with cruciate patterns was significantly higher in Rota. Despite limitations in evaluating specific mechanisms and replication associated with our natural and large-scale comparative approach, correlating variations in web-building and web-decorating behavior with the ecological and ontogenic factors provides a useful model to assess the impacts of environmental changes on island ecosystems.

Keywords: *Argiope appensa,* bird loss, stabilimentum pattern, web decoration, web size

Introduction

Orb-weaving spiders from the families Araneae, Araneidae, Tetragnathidae, and Uloboridae often decorate webs with conspicuous bands of silk (Starks 2002). These web decorations, also called stabilimenta, are built after creation of the web and come in a variety of different shapes and patterns including zigzag discs, crosses, and diagonal or vertical lines (Blackledge 1998). Despite having been studied for more than 100 years, the function of web decorations has been the subject of continued debate.

Several studies agree that these highly visible structures act as visual cues but diverge on whether these cues attract prey, defend against predators, or act as warning devices to avoid inadvertent web damage (reviewed by Herberstein et al. 2000 and Bruce 2005). The prey attraction hypothesis suggests that flying insects are visually attracted to UV light reflected by web decorations (Craig & Bernard 1990, Tso 1996, Herberstein 2000). Craig & Bernard (1990) found that decorated webs had higher rates of prey capture. The anti-predator hypothesis suggests that spiders use web decorations to avoid capture either through camouflage or altering their appearance to make them look larger than they are (Schoener & Spiller 1992, Blackledge 1998). The web protection hypothesis suggests that web decorations serve as visual warnings to prevent birds from unintentionally flying into and damaging webs (Eisner & Nowicki 1983, Horton 1980, Kerr 1993, Blackledge 1998, Blackledge and Wenzel 1999). These hypotheses are not always mutually exclusive; for example, conspicuous web decorations designed to exploit sensory biases of prey could also be used by predators and the avoidance of webs by avian predators consequently prevents web damage.

We predict that investment in web decoration will be less in areas where there is minimal to no risk of web damage caused by birds. Reduction of web decoration size may be a behavioral response towards reduced selection for larger, more elaborate visual warning signals in areas with no selective pressure from birds. Variation may be due to differences in energy allocation in making stabilimenta, *i.e.* if there is no need to make them there is increased selection for those who save energy. Here, we set out to test the hypothesis that spiders will build smaller webs and larger, more complex web decorations in response to the presence of birds. The neighboring islands of Guam and Rota in the Mariana archipelago represent a unique situation to test this hypothesis in a large-scale natural setting. Guam has lost majority of its native avian fauna in the last 50 years as a result of an introduced predator, the brown tree snake, *Boiga irregularis* (Savidge 1987). However, other islands in the Mariana archipelago, including Rota, still possess intact populations of native avian fauna (Conry 1988). Many of the bird species extirpated from Guam, but still present in neighboring islands, have been observed to include spiders in their diet or cause damage to webs by collecting silk to build nests (see Rogers et al. 2012). Kerr (1993) found that *Argiope appensa* webs on Guam were decorated less frequently compared to neighboring islands (Rota, Tinian, and Saipan) and had the lowest recorded frequency compared to 14 different sites worldwide. To date, only very few studies have taken advantage of this unique system (Kerr 1993, Rogers et al. 2012), and no studies have been conducted, at this scale, to look at variations in web decoration size and pattern.

We surveyed forest edges on Guam and Rota to assess the influence of two factors – extrinsic (predator exposure) and intrinsic (spider body size, *i.e.* age) in web-building and web-decorating behavior. We sought to differentiate the size frequency distribution between Guam and Rota as wells as determine whether levels of predator exposure (avifauna) and spider body size (age) can account for variation in web size and web decoration length. Manipulative experiments in the laboratory have shown that spiders subjected to substantial web damage both reduced the size of subsequent webs and increased investment in web decorations (Walter & Elgar 2011). We also compared the frequency of diagonal and cruciate web decoration patterns between islands and between size classes. Although both juvenile and adult *A. appensa* build partial (linear/diagonal) or full cruciate web decorations (Kerr 1993), patterns could vary within species according to a spider's size and age (Herberstein et al. 2000, Uhl 2008) and there are several anti-predator mechanisms that depend on the type of decoration (Schoener & Spiller 1992). Functions of web decoration types remain poorly understood. Despite limitations in evaluating specific mechanisms and replication associated with our natural and large-scale comparative approach, correlating variations in web-building and web-decorating behavior with the ecological and ontogenic factors tested in this study will be valuable in providing some answers to the still unresolved question: what is the purpose of web decorations?

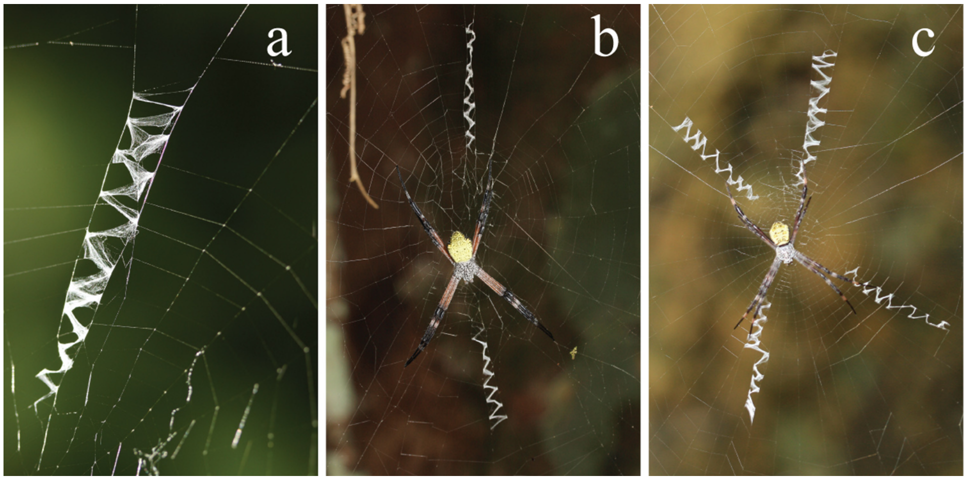

Figure 1. Web decoration *in A. appensa*: (A) close-up of web decoration; (B) linear/ diagonal pattern; (C) cruciate pattern.

Methods

Study Organism and Sites

The orb-weaving spider, *A. appensa* (Walckenaer 1842), is a member of the family Araneidae. Its distribution spans part of Asia, Australia, Vanuatu, New Caledonia, Hawaii, and Micronesia (Suman 1964) and is the dominant spider species in the Marianas archipelago (Kerr 1993, Rogers et al. 2012). The species is sexually dimorphic, wherein females are significantly larger and possess more striking coloration compared to the more cryptic males.

Field census on Guam and Rota were conducted from September to October 2011. Sampling locations were selected based on the presence of web aggregations upon visual inspection of forest edges and roadsides. The island of Guam (13.477721°N, 145.751961°E) is the southernmost island of the Marianas archipelago in Micronesia. Five areas were surveyed on Guam: beach flat forest edge near Togcha Bay, edge of limestone forest near the Guam racetrack and along Anao road, and forest edges within the Guam National Wildlife Refuge in Ritidian. The island of Rota (14.158277°N, 145.207898°E) lies approximately 88 km north of Guam. Surveys were conducted along the roadsides in the village of Songsong, Japanese canyon overlook, northern Sinapalu, and along the edges of vegetation around the Rota Bird Sanctuary.

Survey Methods

Fifty-two webs of female *A. appensa* were surveyed along forest edges on each island. In this study, only decorated webs, 0.5 to 1.5 m from the ground, were evaluated. Abandoned webs were not included in the surveys. Web diam-

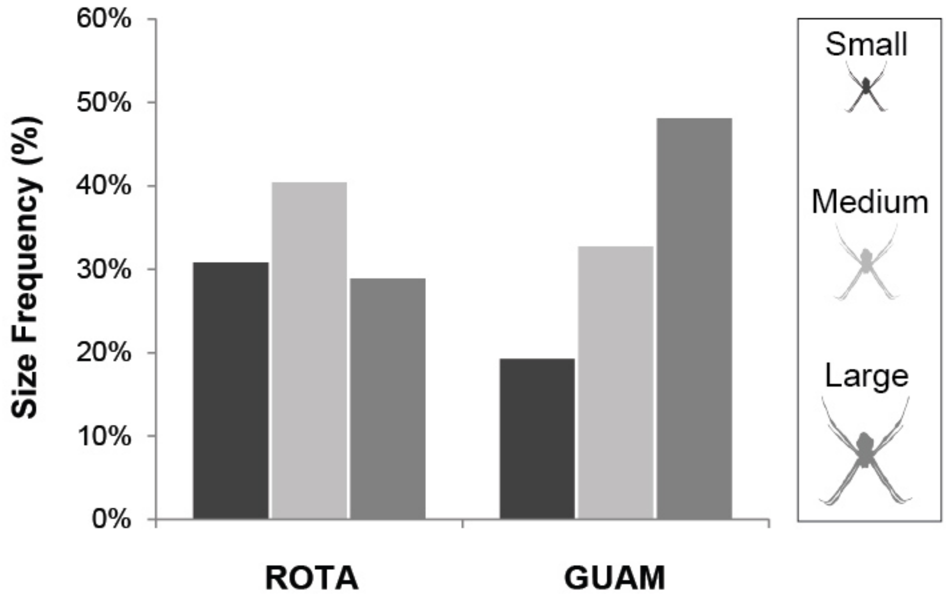

Figure 2. Frequency distribution of spider body size categories in Rota and Guam.

eter was measured as the maximum straight vertical line from the bottom radial line to the top. Only diagonal (Figure 1B) and cruciate (Figure 1C) web decoration patterns that crossed the hub were assessed. Web decoration length was measured using a dial caliper and in the case of cruciate decorations, the longer diagonal line was measured. Total body length of each spider was haphazardly measured and for the purpose of analysis, categorized into the following size classes: small (≤ 10 mm), medium (11-20 mm), or large (>20 mm)

Data Analyses

Differences in spider size frequency distribution between Rota and Guam were analyzed using Chi-Square Test. Two-way Analysis of Variance (ANOVA) was used to test variation in web diameter and web decoration length between islands (two levels: Rota, Guam) and between size classes (three levels: small, medium, large). Web decoration length was square-root transformed to improve normality. Significant tests were followed by pairwise comparisons using Student-Newman-Keul's post hoc test. The relationship between web diameter and web decoration length for each island was analyzed using simple linear regression. Chi-Square Test was also performed to compare frequency of cruciate versus diagonal web decoration patterns between islands.

Results and Discussion

Consistent with previous surveys, it was apparent that *A. appensa* was more abundant on Guam (Rogers et al. 2012), while the frequency of decorated webs was higher in Rota (Kerr 1993). Overall, there was no significant difference in the size frequency distribution of spiders (with decorated webs) sampled between Rota and Guam, $\chi^2_{(df = 2, N = 104)} = 4.306$, $p = 0.116$. Among 104 decorated webs surveyed, medium sized spiders (11-20 mm) were most abundant (40%) in Rota, while large-sized spiders (>20 mm) were most abundant (48%) on Guam (Figure 2). Since sampling was biased towards decorated webs, the size frequency distribution could also indicate that there is no substantial difference in web decoration frequency between juvenile and adult *A. appensa*. Similarly, Kerr (1993) found that the frequency of web decoration in *A. appensa* did not increase with web area, which was used to approximate body length (≈ age). On the other hand, older *Argiope argentata* in the Galapagos have been shown to decorate more frequently than juveniles (Lubin 1975).

Spiders may respond to reduced risk of predation by building larger webs (Li & Lee 2004), which could consequently enhance prey capture (Blackledge & Eliason 2007). Sampling location, representing different levels of predator exposure (high in Rota, low in Guam), did not have a significant effect on web size ($F_{1,98} = 2.517$, $p = 0.116$). Previous surveys also showed no significant inter-island variation in web size (Kerr 1993). Spiders subjected to substantial web damage, similar to that caused by birds, significantly reduced the size of subsequent webs to lower the probability of web damage from oncoming birds (Walter & Elgar 2011) or to reinforce web tension (Nakata 2009). However, substantial damage to individual webs has to be sustained and chronic in order to immediately alter web-building behavior. In this case, the selective pressure may not be strong enough to result in drastic adjustments of web size. Nevertheless, Guam is trending towards slightly larger webs compared to Rota (Figure 3A) and a larger sample size could emphasize this variation, as demonstrated by Rogers et al. (2012), where *A. appensa* webs on Guam were shown to be 50% larger compared to the neighboring islands of Rota, Tinian, and Saipan.

There was a significant ontogenic-related variation in web size ($F_{2,98} = 16.412$, $p < 0.001$), where larger/older individuals built larger webs compared to smaller/younger spiders (Figure 3A). This variation was present in both islands and there was no significant interaction between location and size class ($F_{2,98} = 0.168$, $p = 0.845$). In general, web size correlates with spider size, *i.e.* young orb-weaving spiders build smaller, fine-meshed webs compared to more mature spiders (Witt et al. 1972). Witt & Baum (1960) showed that although web size increased with age, this correlation is not always uniform and there is considerable inter- and intraspecific variation. As the spider grows, the web must

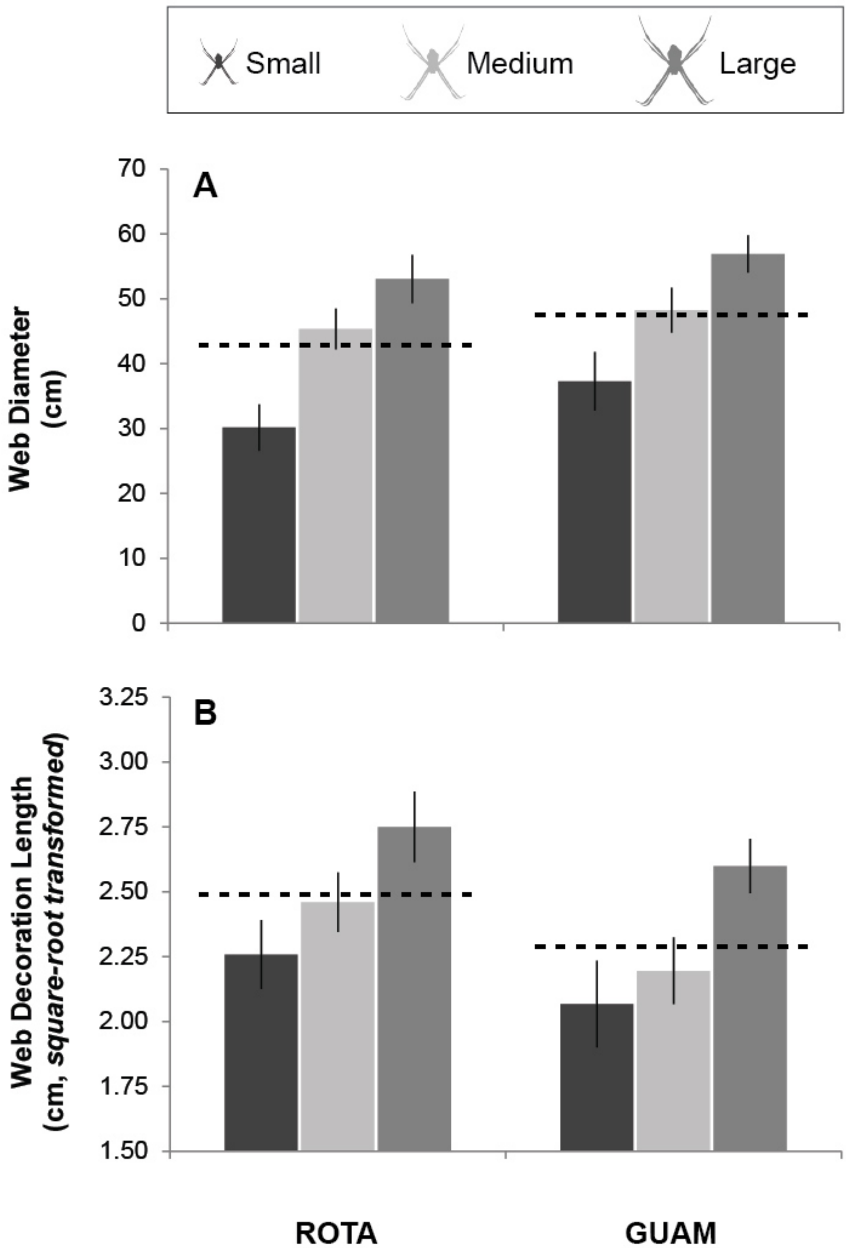

Figure 3. Variation in web-building behavior in *A. appensa* between locations and between spider size class categories, (A) web diameter, SNK: small < medium < large; and (B) web decoration length, SNK: small = medium < large. Dashed lines represent the mean for each location with all the size classes pooled.

also be able to support the increasing weight of the adult spider (Herberstein & Heiling 1999).

Web decorations are produced by spiders that build webs persisting throughout daytime (Eisner & Nowicki 1983) and the bright white silk structures maximize photic simulation of vertebrate eyes so it can be differentiated from a background of soil or foliage (Blackledge 1998) . In dim conditions, the orb-web spider, *Argiope keyserlingi*, construct longer stabilimenta (Herberstein & Fleisch 2003). These suggest that stabilimenta function as visual cues. Using spectrophotometric analyses, Bruce et al. (2005) verified that birds are able to detect stabilimenta from short and long distances and are more effective for advertising the presence of the web rather than camouflaging it. As a visual warning to avoid damage from oncoming birds, it would be advantageous to increase stabilimentum size to enhance its visibility in the presence of more birds in the vicinity. Despite the stark contrast in the abundance of birds between Guam and Rota, web decoration length did not significantly vary between islands ($F_{1,98}$ = 3.510, p = 0.064). Bruce & Herberstein (2006) did not detect any effect of predator cues on the size of decorations in *A. keyserlingi*. Even when exposed to predator cues, juvenile *Argiope versicolor* did not increase the size of web decorations (Li & Lee 2004).

Still, Guam may be trending towards having webs with shorter decorations (Figure 3B), but there might be inadequate power to show these differences due to the relatively low sample size in this study. Alternatively, the relatively larger web decorations in Rota may be linked with the higher frequency of decorated webs and building larger decorations may be a competitive advantage against conspecifics. Walter & Elgar (2011) compared the web-decorating responses of female *A. keyserlingi* to mild mechanical damage, similar to that caused by impacting prey, and to substantial damage that simulated inadvertent damage by non-prey animals, such as birds. Spiders that suffered mild web damage did not change investment in web decoration, but spiders that were subjected to substantial web damage significantly increased the size of decorations of subsequent webs during the 14-day observation period (Walter & Elgar 2011). As mentioned above, the selective pressure in the natural setting has to be substantial, sustained, and chronic in order to elicit immediate changes in web-decorating behavior and it may take more time for responses to be significantly evident.

The most significant web-decorating response to the absence of birds might have something to do with whether or not the spider will decorate webs. As observed during our surveys, decorated webs were harder to find on Guam compared to Rota. Kerr (1993) has clearly shown that *A. appensa* webs on Guam maintained much lower frequency of web decoration (16.40%) compared to conspecific webs in neighboring islands. More recent reports have shown that web decoration frequency on Guam remained generally low, around 15.38%

throughout the island (Delgado 2010, Biometrics Course Special Project, unpub.). Daproza (2010, Biometrics Course Special Project, unpub.) also reported significantly lower web decoration frequencies on Guam compared to the neighboring island of Saipan. The presence of web decorations alone, regardless of its size, may be enough to ward off predators and to advertise webs and prevent inadvertent destruction by birds. This is supported by evidence that decorated webs suffer less damage than undecorated webs (Horton 1980, Eisner & Nowicki 1983, Blackledge & Wenzel 1999; but see Hauber 1998).

The size/age of spiders had a significant main effect on the length of web decorations ($F_{2,98}$ = 7.900, $p < 0.001$). The largest/oldest spiders built significantly longer web decorations compared to small and medium-sized conspecifics (Figure 3B). The same pattern was observed on both islands and there was no significant interaction between islands and size class ($F_{2,98}$ = 0.110, p = 0.896). Web decoration size of *A. appensa* from the Philippines was also positively correlated with the spider's body size (Adamat et al. 2011). Conversely, Kerr (1993) observed that on all islands he surveyed, small juveniles made web decorations with larger and thicker arms than older spiders. Very few studies have looked at ontogenic variation in web decoration size, but rather focused on ontogenic variation in pattern, which will be discussed later. The ontogenic-related variation observed in this study could be related to prey choices (Sensenig et al 2011) and the amount of silk reserves in aciniform glands of spiders (Tso 2004). Silk investment by spiders, increases isometrically with body size (Sensenig et al 2011). The type and size of prey captured by spiders could change as they grow and larger prey captured by adult spiders (Prenter et al. 1999) may be more nutritionally rewarding. Mean decoration length in food-supplemented *Argiope aethera* spiders was significantly longer compared to food deprived conspecifics (Bruce & Herberstein 2005). Furthermore, *A. appensa* that were fed with larger prey built longer web decorations compared to individuals that were starved or fed with smaller prey (Adamat et al. 2011).

Despite parallel trends of increase in web size and web decoration length with spider body size and age (Figure 3), web decoration length was not dependent on the size of the web (Figure 4) in both Rota (r^2=0.022, $F_{(1,50)}$=1.113, p=0.296) and Guam (r^2=0.005, $F_{(1,50)}$=0.249, p=0.620). It was therefore not necessary to standardize web decoration length by the web diameter prior to analysis. Likewise, web size also had no effect on the decoration length of the orb-weaving spider, *Cyclosa octotuberculata* (Gan et al. 2010). Spiders surveyed in Rota built smaller webs but added larger decorations, while spiders on Guam built larger webs with smaller decorations. This is consistent with damage control mechanisms in *A. keyserlingi,* where a high degree of web damage triggers increased investment in silk decorations and reduction of size of subsequent webs (Walter & Elgar 2011). The presence of birds is an environmental stimulus that is more often experienced by spiders in Rota and other islands with intact native avifauna. In the absence of birds on Guam, spiders may be progressively building larger webs but with smaller decorations. Indirectly, the absence of birds could also release spiders from competition for mutual prey and therefore spiders strategically conform web-building and web decorating behavior to maximize prey capture with reduced risk of predation or web damage by birds (Bruce et al. 2001).

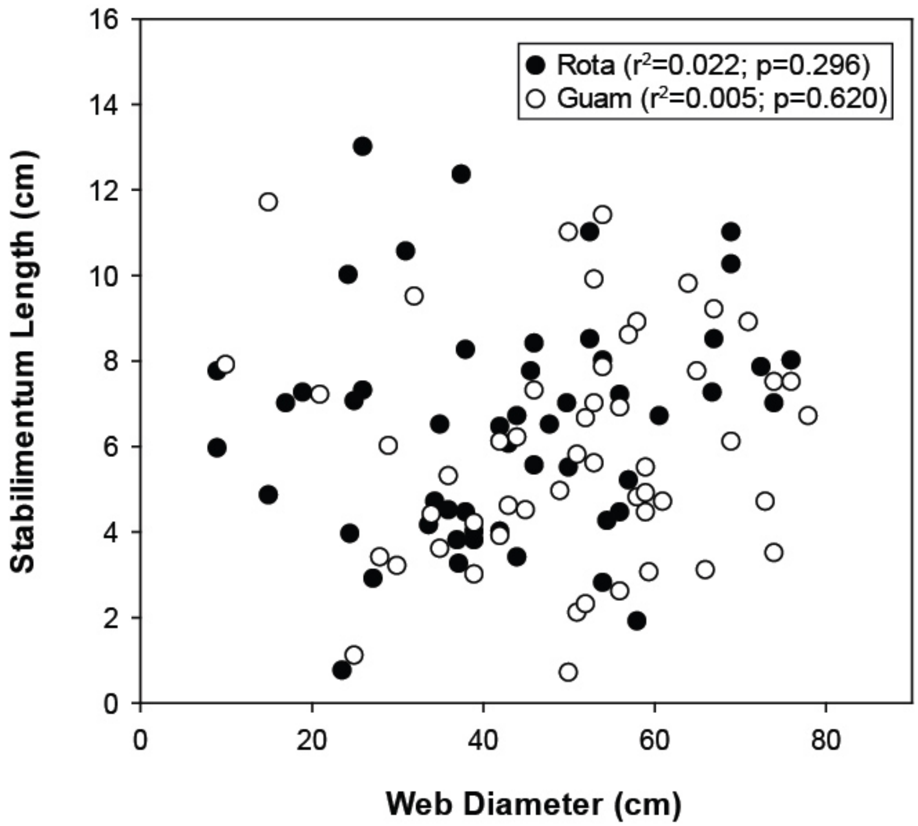

Figure 4. Relationship between web diameter and web decoration length on Rota and Guam.

The specific form or pattern of web decoration is likely to vary across the spider's lifetime and in response to environmental stimuli (Herberstein et al. 2000). The diagonal or linear pattern was the most dominant web decoration in both islands. Nonetheless, the frequency of spiders with cruciate web decorations (Figure 5) was significantly higher ($\chi^2_{[df = 1, N = 104]}$ = 4.308, p = 0.038) in Rota (19.23%) than in Guam (5.77%) . The cruciate pattern may be visually more effective in making the spider appear larger compared to the linear pattern (see

Figure 1B and 1C for comparison). Ancestral character state reconstruction showed that the linear form was ancestral and the cruciate form was derived (Cheng et al. 2010). It has been proposed that the cruciate stabilimenta of *Argiope argentata* extends the apparent length of its legs and make it appear bigger to gape-limited predators (Schoener & Spiller 1992). Indeed, most of the decorations with cruciate pattern were built by the smallest spiders and by medium-sized spiders to a lesser extent (Figure 5). None of the large-sized spiders surveyed built cruciate-patterned decorations. However, *Argiope* spp. display considerable intraspecific ontogenic variation in web decoration pattern (Herberstein et al. 2000) and changes in stabilimentum form have been correlated with maturation (Gan et al. 2010). Smaller *A. argentata* spiders built mainly discoid web decorations while larger spiders constructed at least part of a cruciate-patterned decoration (Uhl 2008).

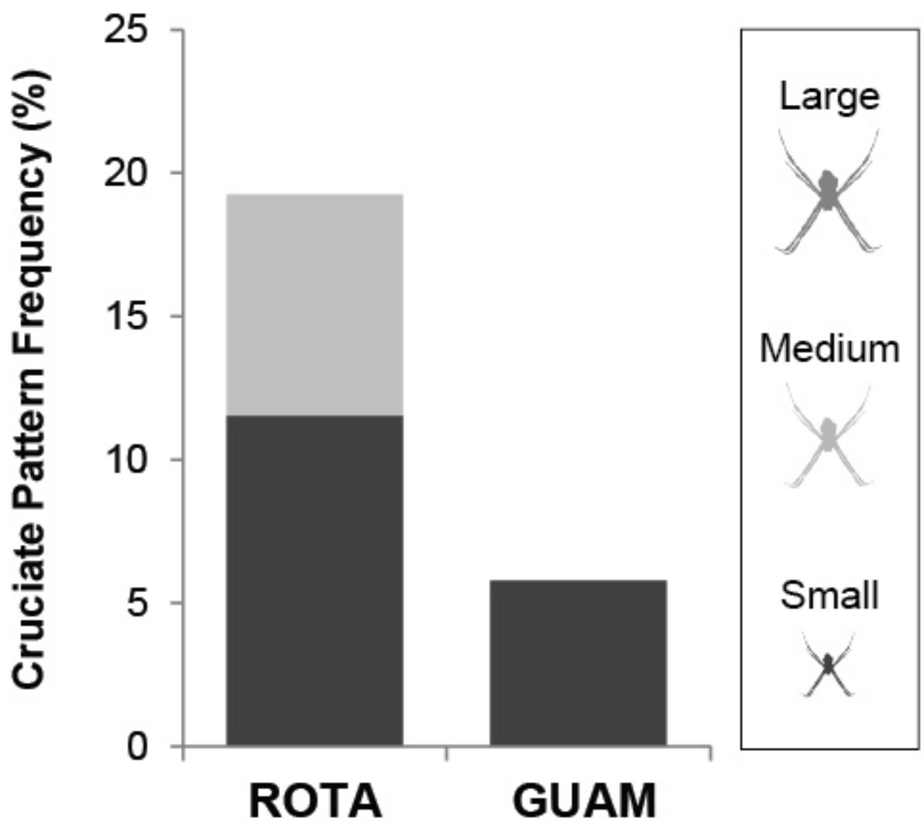

Figure 5. Frequency distribution of cruciate-patterned web decorations from spiders in Rota and Guam. Stacks represent size class of spiders.

Most studies on the variation of web decoration patterns have been focused on prey attraction. Decoration bands in cruciate form were significantly more attractive to insects than those arranged in linear form (Cheng et al. 2010). Bees also responded more quickly to cruciate decorations than to linear decorations (Bruce & Herberstein 2005). If the cruciate pattern is more effective in warding off predators or in attracting prey, then we can expect this to be the more dominant form. However, this is not the case in many *Argiope* populations (Herberstein et al. 2000), which implies that there are underlying costs and trade-offs in building cruciate web decorations. Attracting prey by decorating webs with cruciate patterns goes with a cost of increased predation risk (Bruce et al 2001, Cheng & Tso 2007), so, while cruciate decorations improve foraging success, linear decorations might enhance survival. In addition, the risk of learning prey selects against consistent building of decorations of a fixed form (Craig 1994).

Our study was able to take advantage of a unique natural system to assess variation in web-building and web decorating behavior in response to the presence or absence of birds. We found that web size, web decoration length, and web decoration pattern are correlated with the body size of spiders (ontogenic stage) and with the predator exposure, albeit, to a lesser extent. Variation in web-building and web-decorating behavior seems to involve complicated overlaps between abiotic factors (temperature and light, reviewed in Bruce 2006), heredity (Edmunds 1986), stochastic prey abundance (Tso 1999), and natural selection mediated by the behavior of predator and prey (Kerr 1993). To pinpoint specific and interacting mechanisms will require long-term surveys and well-designed field and laboratory experiments. Variations in the web-building and web-decorating behavior of spiders provide a useful model to assess the impacts of environmental changes on island ecosystems.

Acknowledgements

We would like to thank Dr. Alexander Kerr for helping conceive this project and for sharing his knowledge on arachnids and statistics. We would also like to thank the two anonymous reviewers whose comments have substantially improved this paper. We are also grateful for the hospitality extended to us by the people of Guam and Rota. This paper is dedicated to the memory of Dr. Lynn Raulerson.

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Received 9 Feb. 2012; revised 18 Dec. 2013