Ann. Zool. Fennici 40: 293–303 ISSN 0003-455X
Helsinki 18 June 2003

Resource use within a community of Hawaiian spiders (Araneae: Tetragnathidae)

Todd A. Blackledge[1,2], Greta J. Binford[3] & Rosemary G. Gillespie[1]

[1] *University of California, Berkeley, Environmental Science, Policy and Management, Division of Insect Biology, 201 Wellman Hall, Berkeley, CA 94720-3112 USA*
[2] *Current address: Department of Biology, University of California, Riverside, CA 92521 USA (e-mail: toddbl@citrus.ucr.edu)*
[3] *University of Arizona, Department of Biochemistry and Molecular Biophysics, Tucson, AZ 85721 USA; current address: Department of Biology, Lewis & Clark College, 0615 SW Palatine Hill Rd., Portland, OR 97219, USA*

Received 16 Aug. 2002, revised version received 2 Dec. 2002, accepted 12 Dec. 2002

Blackledge, T. A., Binford, G. J. & Gillespie, R. G. 2003: Resource use within a community of Hawaiian spiders (Araneae: Tetragnathidae). — *Ann. Zool. Fennici* 40: 293–303.

We examined the relationship between web architecture, microhabitat utilization, and prey capture for five sympatric species of spiders (Araneae: Tetragnathidae: *Tetragnatha* Latreille) in Waikamoi Preserve, East Maui, Hawaiian Islands. We found that each species of spider built webs that differed from its congeners in one or more architectural and microhabitat features, and that each species also differed in the types of insect prey they captured. Although the causal mechanisms remain to be tested, we suggest that species-specific differences in web building behaviors could account for the differences found in utilization of prey and microhabitat resources. Furthermore, the ability to construct webs with different architectures may be related to the extraordinary diversification of endemic web-building Hawaiian *Tetragnatha*.

Introduction

The Hawaiian archipelago provides some of the most extraordinary examples of adaptive radiations, due in part to its extreme isolation and the known historical relationships between individual islands (Carlquist 1980, Carson & Clague 1995, Grant 1998). Founder events and geographic isolation between high volcanic peaks have resulted in many spectacular evolutionary radiations through allopatric speciation (Kaneshiro & Boake 1987, Simon 1987, Wagner & Funk 1995). But, there is growing evidence that both natural and sexual selection have also played important roles in generating the amazing endemic diversity found on the Hawaiian Islands, with closely related species often diverging greatly from one another in their ecologies (Wagner & Funk 1995, Roderick & Gillespie 1998).

At least four factors may contribute to diversification of resource use by species within communities (Travisano *et al*. 1995, Schluter 2000). (1) Interspecific competition may lead to the evolutionary specialization of organisms or it may determine how communities are assembled from potential immigrant species (Diamond 1975, Schluter 1994, Losos *et al*. 1998). (2) In a process termed divergent natural selection, organisms may adapt to different optimal combinations of resource use within habitats regardless of interspecific interactions *per se* (Schluter 2000). (3) Predation risk can have significant impacts upon both historical changes in and the current use of resources by lower trophic levels (Lima & Dill 1990, Spiller & Schoener 1994). (4) Finally, chance historical events and clade specific factors may constrain the evolution of community structure in unique ways (Gould 1989). Regardless of the mechanisms by which ecological diversity has arisen, documenting how sympatric species differ in resource utilization plays a valuable role in understanding the stability and function of communities (Polis 1994, Polis & Strong 1996, Tilman 1999).

Spiders are dominant intermediate level predators in most terrestrial ecosystems (Foelix 1996), including Hawaii. In mainland communities there are over 100 families of spiders that display a wide variety of life history strategies (Shear 1986, Coddington & Levi 1991) and that function both as important regulators of arthropod populations and as sources of food for higher trophic levels (Foelix 1996, Wise 1993). In contrast, only 10 families of spiders include species endemic to the Hawaiian Islands, but these spiders constitute some of the most extraordinary examples of evolutionary radiations within the archipelago (Gillespie 1993, Gillespie & Croom 1995, Gillespie *et al*. 1997, Roderick & Gillespie 1998, Garb 1999; *see* also Hormiga 2002). The orb-weaving *Tetragnatha* have been particularly well studied and display a striking contrast between two separate evolutionary lineages (Gillespie 1999). One monophyletic clade of "spiny-leg" *Tetragnatha* has abandoned the use of webs in prey capture altogether and are now cursorial hunters of terrestrial arthropods (Gillespie 1991), while a second monophyletic radiation has retained the web-building habits of their continental ancestors. Within the web-building lineage of *Tetragnatha*, several species can often be found within the same habitat and these sympatric species tend to be each other's closest relatives (Gillespie 1999). Yet, it is unknown whether sympatric orb-weaving *Tetragnatha* differ in their utilization of resources, such as microhabitat or prey, or in the ways in which they construct webs. Because webs act as the interface between spiders and their environment, it is likely that architectural variation in webs would have an important impact upon exploitation of both microhabitat and prey by spiders (Shear 1986, Eberhard 1990, Blackledge & Wenzel 1999, 2001a). Here, we examine the hypothesis that sympatric species of spiders will display interspecific differences in architectures of their orb webs, use of microhabitat, and capture of prey within a community of web-building Hawaiian *Tetragnatha*.

Materials and methods

Natural history of the spiders

The Nature Conservancy of Hawaii's Waikamoi Preserve is located on the northern slope of Haleakala volcano, East Maui. The 2117 ha. preserve ranges in elevation 1300–2600 m and is dominated by stands of 'O'hia trees (*Metrosideros polymorpha* Gaud.) with an understory of ferns (e.g. *Sadleria*). Our research was conducted at two sites within the preserve. The high elevation site consisted of approximately one hectare of mesic forest at 1750 m (20°46´N, 156°14´W). The low elevation mesic forest site was the same approximate size at 1300 m (20°48´N, 156°15´W). Using these two sites allowed us to incorporate all of the species of *Tetragnatha* that construct webs within the preserve (*see* below). Because there was no significant physical barrier between these two sites we combined data from the sites. Although this approach likely obscured some interesting clinal variation, our goal was to determine whether there were broad *inter-specific* differences in web architectures, use of microhabitat, and prey capture so that combining data across both sites would only make it more difficult to refute a null hypothesis of no differences between species.

There are five broadly sympatric species of web-building *Tetragnatha* within Waikamoi preserve (Fig. 1; Gillespie 1992). Three species are relatively abundant and comprise the dominant component of the nocturnal orb-weaving spider guild in Waikamoi, *Tetragnatha eurychasma* Gillespie, *T. filiciphilia* Gillespie, and *T. stelarobusta* Gillespie (Gillespie 1992). *Tetragnatha stelarobusta* is the largest of these

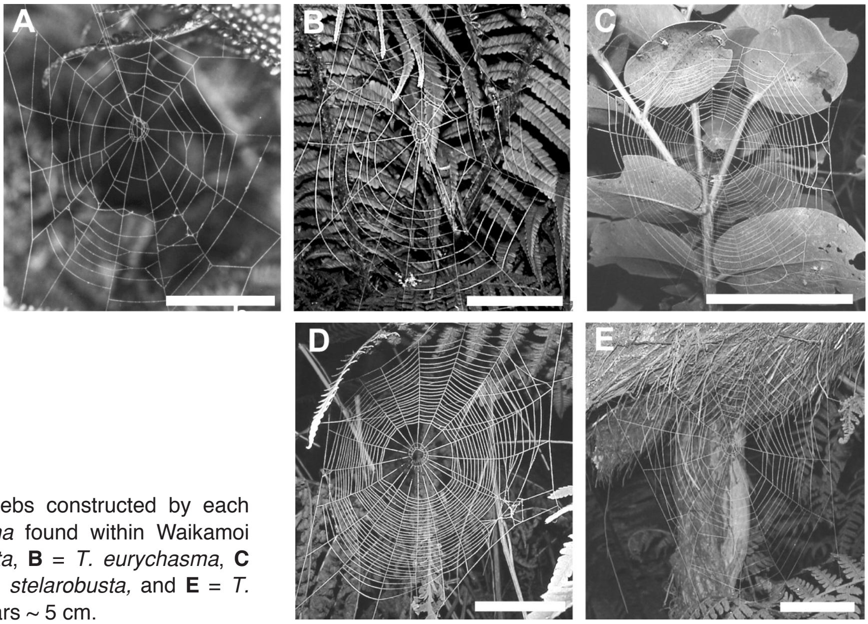

Fig. 1. Typical orb webs constructed by each species of *Tetragnatha* found within Waikamoi Preserve. **A** = *T. acuta*, **B** = *T. eurychasma*, **C** = *T. filiciphilia*, **D** = *T. stelarobusta,* and **E** = *T. trituberculata*. Scale bars ~ 5 cm.

species and is common throughout the preserve. *Tetragnatha eurychasma* is also found throughout Waikamoi preserve but is most abundant at higher elevations. *Tetragnatha filiciphilia* occurs only at lower elevations within the preserve. In some areas these three species overlap in distribution with two relatively rare species, *T. acuta* Gillespie and *T. trituberculata* Gillespie. Due to the rarity of these latter species, we are able to include only limited data on them. While no phylogenetic study has been conducted that includes all five Waikamoi taxa, smaller analyses suggest that they are likely quite closely related to one another because at least *T. filiciphilia*, *T. stelarobusta*, and *T. trituberculata* form a monophyletic clade with respect to other Hawaiian orb-weaving *Tetragnatha* (Gillespie 1999). Penultimate and adult females are easily identified to species in the field by differences in shape and color patterns (Gillespie 1992).

Spider web architecture

Tetragnatha are mostly nocturnal spiders. We therefore conducted all research at night (primarily 10–22 July 2000 and 8–14 July 2001). Because rugged terrain often prevented use of more standardized sampling transects, we performed haphazard searches for spiders. During each night of searching we collected data on every adult and penultimate instar spider located, unless its web was sufficiently damaged to prevent full collection of data. Spiders were collected from webs and the webs were then dusted with cornstarch to enhance visibility of silk. We photographed webs using either a Sony PC110 Digital video camera or a Nikon SLR camera and ringflash. These later photographs were digitized prior to analysis. We measured the vertical and horizontal diameters of webs to the nearest mm in the field to provide scaling factors. For webs at horizontal angles, we designated the longest axis as the "vertical diameter".

We analyzed web photographs on a Microsoft Windows computer using the Scion Image program (ported from NIH Image for the Macintosh by Scion Corporation and available on the Internet at http://www.scioncorp.com). We determined four aspects of web architecture (Fig. 2); capture areas of webs, numbers of radii, lengths of sticky spirals, and mesh widths (spacing between rows of sticky silk). Capture area is the total area of a web delimited by the inner most and outer most spirals of sticky silk (Herberstein & Tso 2000, Blackledge & Gillespie 2002) and was measured directly. Radii are the non-sticky support threads for the sticky spiral, which con-

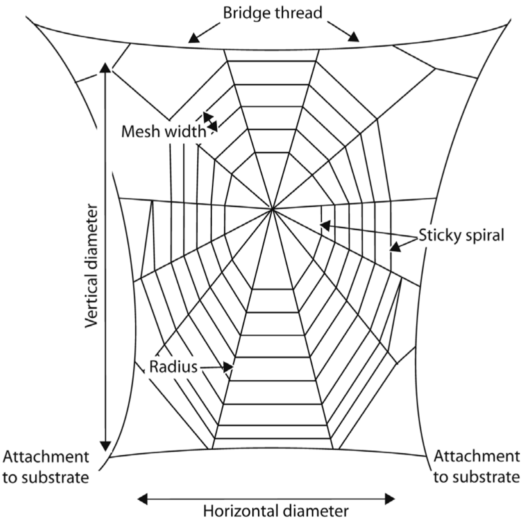

Fig. 2. Illustration of an orb web showing the architectural features we examined. Capture area is the total area of the web covered by the sticky spiral (i.e. delimited by the inner- and outer-most spirals of sticky silk.

verge at the centers of webs, and were counted directly. Total length of sticky silk in a web was estimated using the formula provided by Heiling *et al.* (1998). Average mesh width, or spacing between rows of sticky silk, was computed as Eq. 1.

$$0.5 \times [C_u/(S_u - 1) + C_l/(S_l - 1)] \qquad (1)$$

where C_u and C_l are the lengths of the upper and lower capture areas of webs and S_u and S_l are the numbers of rows of sticky silk in the upper and lower capture areas of webs.

Spider web microhabitat

We measured the microhabitat placement of all webs of *T. eurychasma, T. filiciphilia*, *T. stelarobusta,* and *T. trituberculata* located in the field during July 2001 (no webs of *T. acuta* were located that year). Because orb webs were suspended in three-dimensional spaces, we collected data on the physical parameters defining how individual spiders utilized that space, rather than simply identifying the types of vegetation to which webs were attached. Furthermore, because webs built by different individuals or species were sometimes attached to the same plant, even though these webs clearly did not occupy the same space in the environment. We measured the deviation of webs from a vertical angle to the nearest 10° using a protractor and plumb level. Height of the web above the ground and above the closest vegetation were measured to the nearest cm, allowing us to quantify vertical stratification of species. The total length of the bridge thread (uppermost support thread of the web) was measured to the nearest cm. Bridge thread length provided a measure of how constrained spiders were by distance between substrate attachment points when selecting web sites. We also determined the distance to the nearest vegetation from the front, back, sides, top, and bottom of each web. This allowed us to estimate the total volume of open space surrounding webs, quantifying the openness of different web sites, and to determine the minimum distance to the vegetation from the flat surface of the orb. Finally, we counted the total number of attachments of each web to the substrate and the types of vegetation to which webs were attached. Collectively, these data provide a summary of whether species tended to place webs within dense or open vegetation, at different levels within the forest, etc (*see* also Hoffmaster 1985).

Prey capture by spiders

Because *Tetragnatha* webs are often completely destroyed during prey capture, it was impossible to repeatedly observe individual webs for captured prey (e.g. Blackledge & Wenzel 1999). Instead all spiders found with prey during the sampling of web architecture/microhabitat in 2001 and 2002 were collected (often these spiders were consuming prey in the tattered remains of webs, but some of these data are from spiders for which we also have data on web architecture and microhabitat). In addition, we include data collected during a separate study by GJB on venoms of *Tetragnatha* in Waikamoi Preserve (Binford 2001), which were gathered during June–July 1994 and May–June 1996 at the same localities. We classified prey as belonging to one of four broad morphotype categories; (1) tipulid Diptera (flies) that were gracile bodied with very long legs, (2) non-nematoceran Diptera (flies) with stouter bodies and shorter legs, (3) Lepidoptera (moths), which were stout bodied and covered with scales, and (4) all other prey combined.

Microhabitat and prey availability

We examined the physical parameters of the microhabitat that were available for exploitation by spiders within Waikamoi Preserve. We also measured how microhabitat features were associated with the availability of the insect prey of spiders. We randomly selected 57 sites for "artificial web" sticky traps on the same days and in the same areas where we sampled spiders in 2001. Artificial webs were randomly located 25–175 cm above the ground, in randomly chosen directions within 0.5 to 1.5 m of another web site. For each artificial web we measured the same set of parameters associated with its microhabitat as for real spider webs, except total number of attachment points, which could not be estimated. We measured the bridge thread length as the shortest possible distance between two pieces of substrate that could support the artificial web at its location. Thus, we could characterize the variation in the physical features that spiders potentially could use to construct webs.

Sheets of clear plastic (900 cm^2), constructed from overhead transparency sheets cut in half and coated on both sides with tangle-trap adhesive, were placed at each artificial web site (n = 57). Traps were placed at random angles at the same sites and on the same days that webs were sampled in 2001 and allowed to capture prey for approximately 7 hours (dusk to dawn). Each trap and site was used for only a single night and all traps were placed between 19:30–20:30. This allowed us to determine how individual types of prey were associated with variation in microhabitat. All insects captured in these artificial webs were identified to the same morphotypes described above.

Data analysis

Data analysis was conducted using Statistica 6.0 software on a PC computer (Statsoft 2001). We used ANOVAs to compare capture area, number of radii, length of sticky spiral, and mesh width between species. To determine if differences in spider sizes alone were responsible for interspecific variation in web architectures, we used a second set of ANOVAs that included carapace lengths of spiders as a covariate. We made planned post-hoc comparisons between each pair of species for each architectural feature using Least Significant Differences tests. Although included in the graphs, data on *T. trituberculata* were excluded from all statistical tests due to the small sample size (n = 3).

Microhabitat use by spiders and microhabitat availability data were not normally distributed. Therefore, we used Kruskal-Wallis ANOVAs to test whether the medians of each microhabitat parameter differed between species. We then used Kolmogorov-Smirnov tests to compare the distributions of each microhabitat parameter between all species pairs and between each species and our microhabitat availability data (*see* below), using a Bonferroni method correction for a global $p < 0.05$. Because the Bonferroni method correction is relatively conservative (Sokal & Rohlf 1998), we report pairwise differences that are marginally significant (i.e. that would have been significant if a total of five rather than six pairwise comparisons had been made). This methodology was also used to compare how microhabitat features varied across different types of available prey.

We used G-tests to compare the frequencies of morphotypes captured by each pair of species of spiders and to compare prey captured by each species of spider with the overall prey availability estimated from our artificial web traps (*see* below). All tests were performed at a global $p <$ 0.05 using Bonferroni method corrections (Sokal and Rohlf 1998).

Results

Spider web architecture

Capture area, sticky spiral length, mesh width, and number of radii all varied significantly among species (Fig. 3; one-way ANOVA comparisons across all species except *T. tritubercu-*

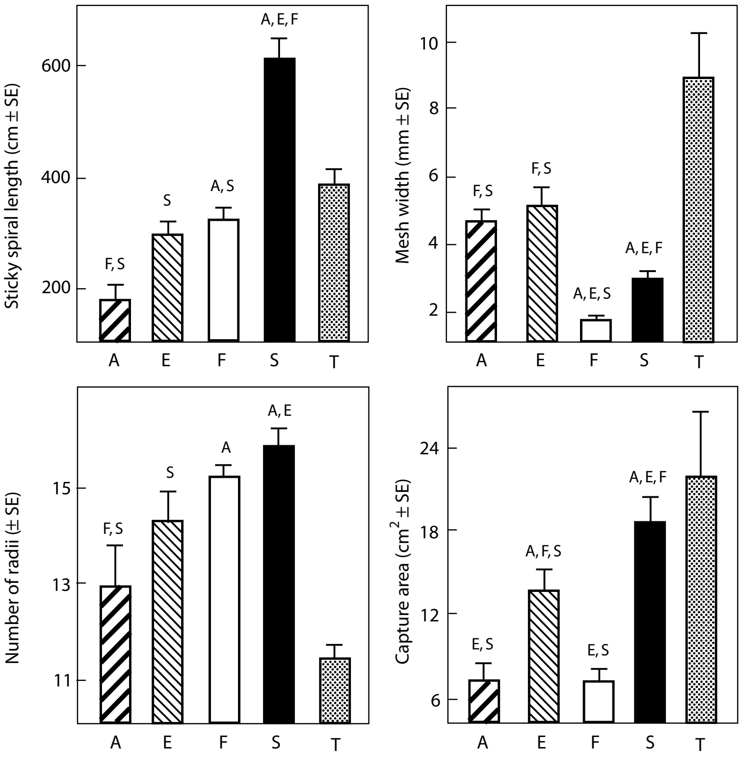

Fig. 3. Variation in web architecture between five sympatric species of *Tetragnatha* (mean ± SE). A = *T. acuta* (*n* = 12), E = *T. eurychasma* (*n* = 20), F = *T. filiciphilia* (*n* = 27), S = *T. stelarobusta* (*n* = 27), and T = *T. trituberculata* (*n* = 3). Letters above each column denote significant pair wise differences in post-hoc comparisons using Least Significant Differences tests ($p < 0.05$). *Tetragnatha trituberculata* was excluded from pair-wise comparisons due to the small sample size.

lata, df = 4, 84, all $p < 0.0001$). These differences were significant even after we controlled for possible allometric effects of spider size by including carapace lengths of spiders as covariates in the ANOVAs ($p < 0.05$, individual tests not shown). Post hoc comparisons revealed that at least one pair of species differed significantly for each architectural feature examined, at a global $p < 0.05$ (Fig. 3). *Tetragnatha stelarobusta* and *T. trituberculata* constructed the largest webs, but *T. stelarobusta* used a much longer sticky spiral and consequently had a narrower mesh width. *Tetragnatha filiciphilia* and *T. acuta* constructed the smallest webs but *T. acuta* constructed webs that had wider mesh widths. *Tetragnatha eurychasma* was generally intermediate in its web architecture (Fig. 1).

Spider web microhabitat

We were only able to gather microhabitat data for the three dominant species of *Tetragnatha* in Waikamoi Preserve, *T. eurychasma*, *T. filiciphilia*, and *T. stelarobusta* (Fig. 4), as well as three observations for *T. trituberculata*. Angles of webs, heights of webs above the ground, lengths of bridge threads, and minimum distances of faces of webs to the vegetation all varied significantly between species, but numbers of attachments, heights of webs above vegetation, and total volume of open spaces around webs did not vary between species (Table 1). There was also little differentiation among species in the

Table 1. Kruskal-Wallis ANOVA (df = 2) comparisons of the microhabitat placement of webs between the three dominant species of *Tetragnatha* within Waikamoi Preserve, East Maui.

Microhabitat feature	*H*	*p*
Height above ground (cm)	9.5	< 0.01
Height above vegetation (cm)	1.3	n.s.
Total openness (m^3)	1.4	n.s.
Min. distance to web face (cm)	19.6	< 0.0001
Bridge thread length (cm)	24.9	< 0.0001
Angle from vertical (°)	13.2	< 0.001
Number of attachment points	4.9	n.s.

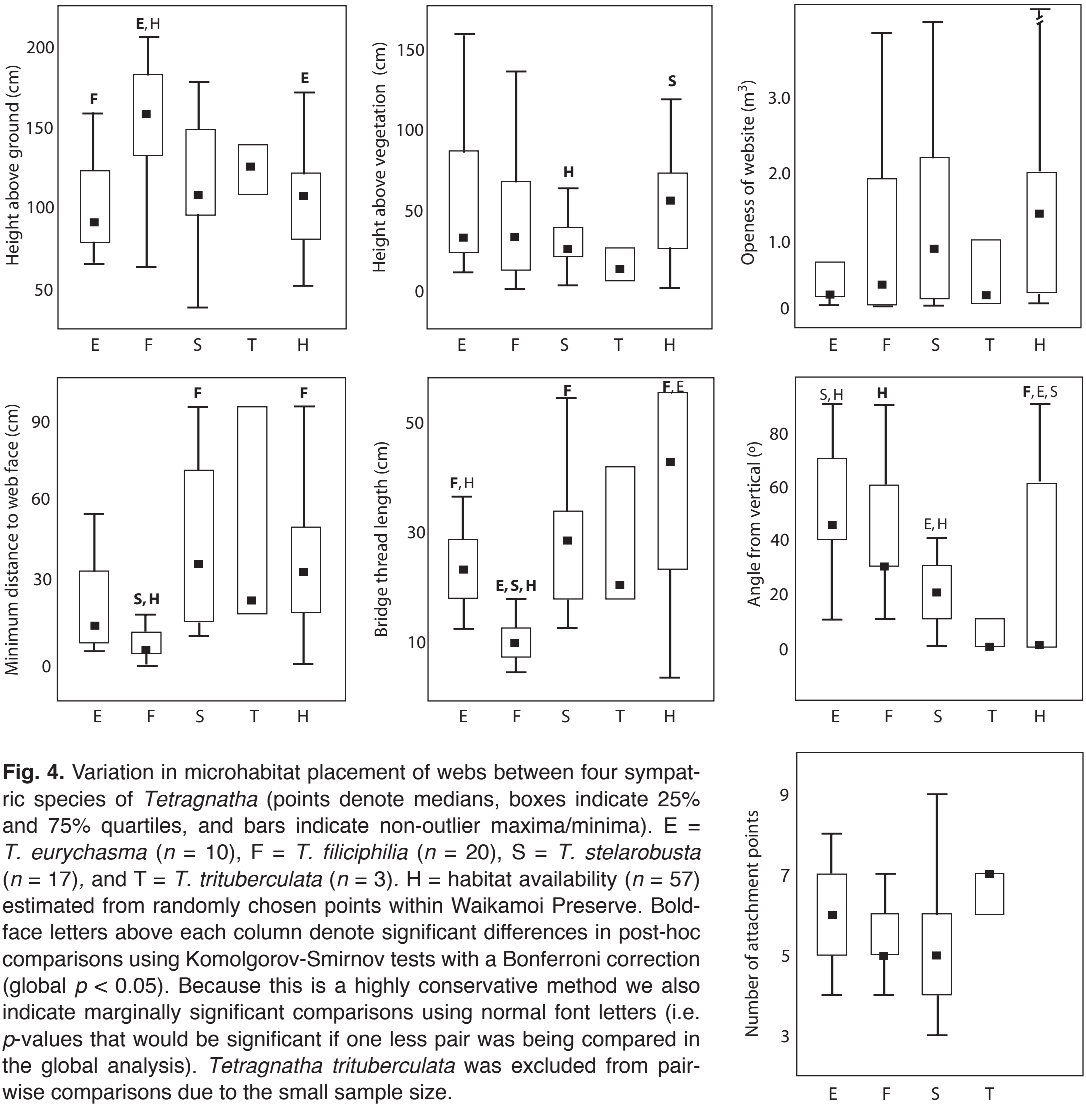

Fig. 4. Variation in microhabitat placement of webs between four sympatric species of *Tetragnatha* (points denote medians, boxes indicate 25% and 75% quartiles, and bars indicate non-outlier maxima/minima). E = *T. eurychasma* (*n* = 10), F = *T. filiciphilia* (*n* = 20), S = *T. stelarobusta* (*n* = 17), and T = *T. trituberculata* (*n* = 3). H = habitat availability (*n* = 57) estimated from randomly chosen points within Waikamoi Preserve. Boldface letters above each column denote significant differences in post-hoc comparisons using Komolgorov-Smirnov tests with a Bonferroni correction (global $p < 0.05$). Because this is a highly conservative method we also indicate marginally significant comparisons using normal font letters (i.e. *p*-values that would be significant if one less pair was being compared in the global analysis). *Tetragnatha trituberculata* was excluded from pairwise comparisons due to the small sample size.

types of vegetation to which they attached webs. *Tetragnatha filiciphilia* tended to build webs that were higher above the ground than the other species and that were attached closer to the vegetation with very short bridge threads. *Tetragnatha filiciphilia* webs also varied greatly from vertical to horizontal orientation. *Tetragnatha stelarobusta* constructed mostly vertical webs whose faces were oriented toward open spaces in the vegetation (Fig. 4). *Tetragnatha eurychasma* built the lowest webs, which were intermediate in their openness in the vegetation (Fig. 4). The three *T. trituberculata* webs observed were all placed along the sides of tree trunks.

Prey capture by spiders

We collected 151 prey captured by the three dominant species in the guild, *T. eurychasma*, *T. filiciphilia*, and *T. stelarobusta*. 70% of captured prey could be classified into one of three broad morphotype categories; (1) tipulid Diptera, (2) non-tipulid Diptera, and (3) Lepidoptera (Fig. 5). The distribution of prey captured by each species differed significantly from other species and from that generally available in the environment for all comparisons except *T. eurychasma* with *T. filiciphilia* (Fig. 5). *Tetragnatha stelarobusta* captured a much higher proportion of Lepi-

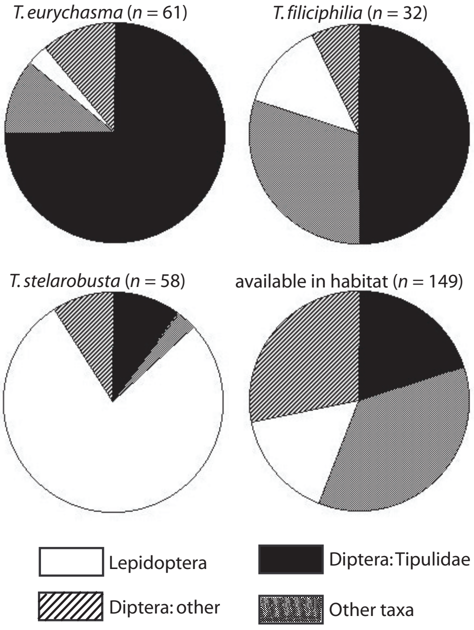

Fig. 5. Prey captured by the three dominant *Tetragnatha* species within Waikamoi Preserve, East Maui. Captured prey differed significantly from that available in the environment and from other species for all comparisons except *T. filiciphilia* with either *T. eurychamsa* or the environment (*G*-tests, df = 3, using a Bonferroni correction for a global p at least < 0.05). Availability of prey in the habitat was assayed using 57 sticky traps randomly placed in the same two sites where spiders were sampled.

doptera (moths) than did *T. eurychasma* and *T. filiciphilia*. Both *T. eurychasma* and *T. filiciphilia* captured a higher proportion of tipulid Diptera than were present in the environment.

Microhabitat and prey availability

Microhabitat characteristics had a significant relationship with the types of prey available to spiders (Table 2). Heights of webs, heights of webs above the vegetation, and total openness of webs all strongly differed between prey morphotypes. Angle and distance to the face of the artificial web traps also differed between prey morphotypes. In particular, small Diptera (i.e. non-tipulid taxa) tended to occur lower in the forest and closer to vegetation than did other prey.

Discussion

The shapes of spider webs directly influences how spiders utilize microhabitat and prey resources (Shear 1986, Eberhard 1990, Blackledge & Wenzel 1999, 2001a). We found that each species of orb-weaving *Tetragnatha* in an East Maui wet forest ecosystem differed significantly from its congeners not only in one or more aspects of microhabitat (Fig. 4) and prey captured (Fig. 5), but also in web architecture (Fig. 3). However, our study does not test the extent to which web architecture plays a causal role in species differences in microhabitat or prey cap-

Table 2. Relationship between microhabitat and available prey within Waikamoi Preserve, East Maui.

	Proportion of available prey			
Microhabitat feature	Diptera: Tipulidae *n* = 29	Diptera: other *n* = 53	Lepidoptera *n* = 23	Other taxa *n* = 44
Angle of trap (°)*	10 (0, 80)	60 (36, 80)	10 (0, 60)	36 (0, 70)
Height above ground (cm)****	104 (76, 140)^{2}	56 (56, 86)^{1,3,4}	81 (74, 114)^{2,4}	130 (86, 145)^{2,3}
Height above vegetation (cm)****	64 (53, 76)^{2}	36 (15, 46)^{1}	58 (8, 69)	53 (36, 76)^{2}
Bridge thread length (cm)	53 (30, 58)	46 (41, 56)	43 (30, 66)	53 (30, 79)
Total openness (m^{3}) ***	0.85 (0.48, 2.44)	0.52 (0.03, 0.85)^{4}	0.44 (0.11, 1.70)	1.73 (0.48, 2.52)^{2}
Min. distance to web face (cm)*	20 (10, 33)^{2,4}	43 (5, 43)^{1}	23 (20, 43)	43 (20, 91)^{1}

Medians (25%, 75% quartiles). * denotes significance using Kruskal-Wallis ANOVA: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$, **** $p < 0.001$. Superscripts indicate significant differences in post-hoc comparisons using Komolgorov-Smirnov tests with a Bonferroni correction (global $p < 0.05$). ^{1} Diptera: Tipulidae, ^{2} Diptera: other, ^{3} Lepidoptera, ^{4} Other taxa. Post-hoc comparisons are identical using Mann-Whitney *U*-tests, except for minimum distance to web face, which shows groups 2 and 4 being different.

ture, nor whether those differences have evolved due to competitive interactions, divergent selective pressures, predation risk, or chance effects.

Clearly, microhabitat and prey resources are not completely independent of one another and we found significant variation in the types of prey available to spiders as a function of microhabitat (Table 2). Yet, there is little evidence that differences in prey capture between species of spiders were due solely to effects of microhabitat. For instance, *T. stelarobusta* captured predominately Lepidoptera while *T. eurychasma* captured primarily tipulid Diptera (Fig. 5), but there was no detectable difference in the microhabitat preferences of these two types of prey (Table 2). Instead differences in web architectures could explain why *T. stelarobusta* captures moths and *T. eurychasma* captures tipulid flies (e.g. Olive 1981). Moths are particularly challenging prey for spiders because their scales prevent moths from sticking to webs (Eisner *et al*. 1964). Thus, moth-feeding spiders often build specialized “ladder” webs with very large and tight sticky spirals that gradually rub off the slippery scales (Stowe 1986). Webs built by *T. stelarobusta* were larger and contained at least 100% more sticky silk than those of other species, which is consistent with the evolutionary elaboration of “ladder” web, although *T. stelarobusta* webs do not exhibit the same high degree of web and hub asymmetry (Blackledge & Gillespie 2002) exhibited by ladder webs.

Uniqueness of Hawaiian spider guilds

In continental ecosystems, guilds of web-foraging spiders are composed of species from many genera that are only distantly related to one another. These sympatric species differ in phenologies, microhabitats of webs (Hoffmaster 1985), reactions to intercepted prey (Olive 1980), and architectures of webs (Eberhard 1990; Wise 1993), although it is typically unclear what processes led to the evolution of these differences (Wise 1993). *Tetragnatha* is normally only one component of mainland orb-weaving spiders guilds, but the genus is worldwide in distribution and species are considered to be homogeneous in both web architectures and predatory tactics (Levi 1981). Also, like other spiders, when multiple species of *Tetragnatha* do occur within the same habitat, they display strong inter-specific differences in seasonal abundances and build webs within broadly different microhabitats (Yoshida 1981, Williams *et al*. 1995, Aiken & Coyle 2000).

In contrast, communities of nocturnal orb-weaving spiders in the Hawaiian Islands are filled exclusively by species from a single endemic evolutionary lineage of *Tetragnatha*, with the exception of one additional endemic species of *Tetragnatha* (*T. hawaiensis*) from a possible separate introduction to the islands (Gillespie *et al*. 1994). Furthermore, multiple species of orb-weaving *Tetragnatha* co-occur within individual habitats and have overlapping phenologies so that different species will construct orb webs within centimeters of one another (Gillespie 1992; pers. obs.). This suggests that differences in the microhabitat placement of webs and in the architectural features of webs related to capture of prey might be especially important for coexistence of sympatric species of Hawaiian *Tetragnatha* if competition occurs between species. However, similar ecological differentiation of resource use within guilds may also result from divergent natural selection where species evolve toward different optimal combinations of resource use (Losos 1990, Losos & Irschick 1994, Schluter 1994, Schluter 2000), such as adaptations of web architecture that allow exploitation of moths (Stowe 1986), or even from predation pressures within habitats (Blackledge & Wenzel 1999, 2001b, Blackledge *et al*. 2003). Ultimately, experimental study will be necessary to test these hypotheses.

Behavioral diversification and adaptive radiation

In addition to the web-building lineage studied here, there has been a second evolutionary radiation of *Tetragnatha* across the Hawaiian Archipelago by members of the “spiny leg” clade (Gillespie 1991). “Spiny leg” *Tetragnatha* have lost the ability to construct webs and now function as cursorial hunters within the same habitats as the web-building *Tetragnatha*. Rates of speciation appear to be much lower in the "spiny leg" clade compared to the web-building clade (Gillespie & Croom 1995, Gillespie 1999). One potential explanation is that sedentary web-building spiders can subdivide habitats more finely than cursorial spiders thereby facilitating speciation (Gillespie & Croom 1995, Gillespie 1999). However, the diversification of web building behaviors that we found within Waikamoi Preserve suggests an alternative or additional explanation for this disparity in speciation rates. Evolution of differences in web architecture could facilitate species richness by allowing exploitation of increased diversity of resources, reducing competition, or altering risk of predation.

Summary

Our study demonstrates that ecological diversification has occurred within a community of closely related endemic Hawaiian spiders, but the causal factors of that differentiation remain to be addressed. Ecological diversification has played an important role in the adaptive radiations of many endemic Hawaiian organisms (Wagner and Funk 1995, Roderick and Gillespie 1998), and this study is the first documentation that such diversification has occurred within the endemic web-building *Tetragnatha*. Future research should allow us to address questions regarding the relationship between community structure of these spiders and their evolutionary radiation. In particular, has there been a parallel structuring of orb-weaving spider niches across different Hawaiian habitats, as has been suggested for the non-web building "spiny-leg" spiders? Ultimately, such studies will provide further insight into the role ecological diversification has played in the evolution of the unique biota of the Hawaiian Islands.

Acknowledgments

Giao Hang assisted greatly with the collection of data in the field. Ryan Schwarz, Harold Greeney, and David Preston helped with prey sampling and identification. We thank Eric Nishibayashi and the other staff of The Nature Conservancy of Hawaii, Betsy Gagne of the Hawaii State Department of Land and Natural Resources, Ellen Van Gelder (Biological Resources Division, USGS), and the staff of Haleakala National Park for facilitating our studies.

References

Aiken, M. & Coyle, F. A. 2000: Habitat distribution, life history and behavior of Tetragnatha spider species in the Great Smoky Mountains National Park. — *J. Arachnol.* 28: 97–106.

Binford, G. J. 2001: Differences in venom composition between orb-weaving and wandering Hawaiian *Tetragnatha* (Araneae). — *Biol. J. Linn. Soc.* 74: 581–595.

Blackledge, T. A. & Wenzel, J. W. 1999: Do stabilimenta in orb webs attract prey or defend spiders? — *Behav. Ecol.* 10: 372–376.

Blackledge, T. A. & Wenzel, J. W. 2001a: State-determinate foraging decisions and web architecture in the spider *Dictyna volucripes* (Araneae, Dictynidae). — *Ethol. Ecol. Evol.* 13: 105–113.

Blackledge, T. A. & Wenzel, J. W. 2001b: Silk mediated defense by an orb web spider against predatory mud-dauber wasps. — *Behaviour* 138: 155–171.

Blackledge, T. A. & Gillespie, R. G. 2002: Estimation of capture areas of spider webs in relation to web asymmetry. — *J. Arachnol.* 30: 70–77.

Blackledge, T. A., Coddington, J. A. & Gillespie, R. G. 2003: Are three-dimensional spider webs defensive adaptations? — *Ecol. Lett.* 6: 13–18.

Carlquist, S. 1980: *Hawaii, a natural history*. — National Tropical Botanical Garden, Lawaii.

Carson, H. L. & Clague, D. A. 1995: Geology and biogeography of the Hawaiian Islands. — In: Wagner, W. L. & Funk, V. A. (eds.), *Hawaiian biogeography: evolution on a hot spot archipelago*: 14–29. Smithsonian Institution Press, Washington, D.C.

Coddington, J. A. & Levi, H. W. 1991: Systematics and evolution of spiders (Araneae). — *Annu. Rev. Ecol. Syst.* 22: 565–592.

Diamond, J. M. 1975: Assembly of species communities. — In: Cody, M. L. & Diamond, J. M. (eds.), *Ecology and evolution of communities*: 342–444. Belknap Press, Cambridge.

Eberhard, W. G. 1990: Function and phylogeny of spider webs. — *Annu. Rev. Ecol. Syst.* 21: 341–372.

Eisner, T., Ettersha, G. & Alsop, R. 1964: Adhesiveness of spider silk. — *Science* 146: 1058–1061.

Foelix, R. F. 1996: *Biology of spiders*. — Oxford University Press, New York.

Garb, J. E. 1999: An adaptive radiation of Hawaiian Thomisidae: biogeographic and genetic evidence. — *J. Arachnol.* 27: 71–78.

Gillespie, R. G. 1991: Hawaiian spiders of the genus *Tetragnatha*: I. Spiny leg clade. — *J. Arachnol.* 19: 174–209.

Gillespie, R. G. 1992: Hawaiian spiders of the genus *Tetragnatha*: II. Species from natural areas of windward east Maui. — *J. Arachnol.* 20: 1–17.

Gillespie, R. G. 1993: Biogeographic patterns of phylogeny in a clade of endemic Hawaiian spiders (Araneae, Tetragnathidae). — *Mem. Queensl. Museum* 33: 519–526.

Gillespie, R. G. 1999: Comparison of rates of speciation in web-building and non-web- building groups within a Hawaiian spider radiation. — *J. Arachnol*. 27: 79–85.

Gillespie, R. G., Croom, H. B. & Palumbi, S. R. 1994: Multiple origins of a spider radiation in Hawaii. — *Proc. Nat. Acad. Sci. USA* 91: 2290–2294.

Gillespie, R. G. & Croom, H. B. 1995: Comparison of speciation mechanisms in web-building and non-web-building groups within a lineage of spiders. — In: Wagner, W. L. & Funk, V. A. (eds.), *Hawaiian biogeography: evolution on a hot spot archipelago*: 121–146. Smithsonian Institution Press, Washington, D.C.

Gillespie, R. G., Croom, H. B. & Hasty, G. L. 1997: Phylogenetic relationships and adaptive shifts among major clades of *Tetragnatha* spiders (Araneae: Tetragnathidae) in Hawai'i. — *Pac. Sci*. 51: 380–394.

Gould, S. J. 1989: *Wonderful life: the Burgess Shale and the nature of history*. — New York: Norton.

Grant, P. R. (ed.) 1998: *Evolution on islands*. — Oxford University Press, Oxford.

Heiling, A. M., Herberstein, M. E. & Spitzer, G. 1998: Calculation of capture thread length in orb webs: Evaluation of new formulae. — *Ann. Entomol. Soc. Am*. 91: 135–138.

Herberstein, M. E. & Tso, I. M. 2000: Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneoidea, Araneae). — *J. Arachnol*. 28: 180–184.

Hoffmaster, D. K. 1985: Resource breadth in orb-weaving spiders — a tropical-temperate comparison. — *Ecology* 66: 626–629.

Hormiga, G. 2002: *Orsonwelles*, a new genus of giant linyphiid spiders (Araneae) from the Hawaiian Islands. — *Invertebr. Syst*. 16: 369–448.

Kaneshiro, K. Y. & Boake, C. R. B. 1987: Sexual selection and speciation: issues raised by Hawaiian *Drosophila*. — *Trends Ecol. Evol*. 2: 207–212.

Levi, H. W. 1981: The American orb-weaver genera Dolichognatha and Tetragnatha north of Mexico (Araneae: Araneidae, Tetragnathinae). — *Bull. Mus. Comp. Zool*. 149: 271–318.

Lima, S. L. & Dill, L. M. 1990: Behavioral decisions made under the risk of predation — a review and prospectus. — *Can. J. Zool*. 68: 619–640.

Losos, J. B. 1990: A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. — *Evolution* 44: 558–569.

Losos, J. B. & Irschick, D. J. 1994: Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. — *Evolution* 48: 1786–1798.

Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K. & Rodriguez-Schettino, L. 1998: Contingency and determinism in replicated adaptive radiations of island lizards. — *Science* 279: 2115–2118.

Olive, C. W. 1981: Co-adapted foraging traits in a guild of orb-weaving spiders. — *Oecologia* 49: 88–91.

Polis, G. A. 1994: Food webs, trophic cascades and community structure. — *Aust. J. Ecol*. 19: 121–136.

Polis, G. A. & Strong, D. R. 1996: Food web complexity and community dynamics. — *Am. Nat*. 147: 813–846.

Roderick, G. K. & Gillespie, R. G. 1998: Speciation and phylogeography of Hawaiian terrestrial arthropods. — *Mol. Ecol*. 7: 519–531.

Schluter, D. 1994: Experimental evidence that competition promotes divergence in adaptive radiation. — *Science*. 266: 798–801.

Schluter, D. 2000: Ecological character displacement in adaptive radiation. — *Am. Nat*. 156: S4–S16.

Schoener, T. W. 1974: Resource partitioning in ecological communities. — *Science*. 185: 27–39.

Shear, W. A. (ed.) 1986: *Spiders, webs, behavior, and evolution*. — Stanford University Press, Stanford.

Simon, C. 1987: Hawaiian evolutionary biology: an introduction. — *Trends Ecol. Evol*. 2: 175–178.

Sokal, R. R. & Rohlf, F. J. 1998: *Biometry*. — W. H. Freeman and Co, New York.

Spiller, D. A. & Schoener, T. W. 1994: Effects of top and intermediate predators in a terrestrial food-web. — *Ecology* 75: 182–196.

Statsoft, Inc. 2001: *Statistica (data analysis software system), version 6.0 computer program* — Statsoft, Inc.

Stowe, M. K. 1986: Prey specialization in the Araneidae. — In Shear, W. A. (ed.), *Spiders, webs, behavior, and evolution*: 101–131. Stanford University Press, Stanford.

Tilman, D. 1999: The ecological consequences of changes in biodiversity: A search for general principles. — *Ecology*. 80: 1455–1474.

Tokeshi, M. 1999: *Species coexistence: ecological and evolutionary perspectives*. — Malden, Blackwell Science Ltd.

Travisano, M., Mongold, J. A., Bennett, A. F. & Lenski, R. E. 1995: Experimental tests of the role of adaptation, chance, and history in evolution. — *Science* 267: 87–90.

Wagner, W. L. & Funk, V. A. (eds.) 1995: *Hawaiian biogeography: evolution on a hot spot archipelago*. — Smithsonian Institution Press, Washington, D.C.

Williams, D. D., Ambrose, L. G. & Browning, L. N. 1995: Trophic dynamics of two sympatric species of riparian spiders (Araneae, Tetragnathidae). — *Can. J. Zool*. 73: 1545–1553.

Wise, D. H. 1993: *Spiders in ecological webs*. — Cambridge University Press, New York.

Yoshida, M. 1981: Preliminary study on the ecology of three horizontal orb weavers, *Tetragnatha praedonia, T. japonica*, and *T. pinicola* (Araneae: Tetragnathidae). — *Acta Arachnologica* 30: 49–64.