

COLORATION IN RELATION TO ECOLOGY IN THE ASIAN SPINY-BACKED SPIDER, *THELACANTHA BREVISPINA* (ARANEAE, ARANEIDAE) ON MOOREA, FRENCH POLYNESIA

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Abstract. Color polymorphism is a widespread phenomenon in many arthropods, including spiders. The persistence of these visible, readily measured polymorphisms over time suggests that they carry adaptive functions and thus are maintained by natural selection. Studying polymorphism is useful for examining evolution in action and the different modes of selection operating to maintain different morph patterns. The color polymorphic spiny-backed spider, *Thelacantha brevispina*, was surveyed on Moorea, French Polynesia to understand distribution, prey abundance, and density across coastal and forest habitats. In addition, split-brood and laboratory reciprocal transplant experiments were conducted to determine whether coloration was due to genes or a result of phenotypic plasticity. Quantitative field surveys revealed a negative relationship between spider density and prey abundance, with lower prey counts in coastal habitats but prey yielded higher energy value. Spiders were found on a variety of habitats with diverse prey species. The split-brood design showed that a genetic origin of coloration is likely with strong maternal effects and distinct color differences among sites. The reciprocal transplant confirmed the lack of a plastic response to rearing habitats. The results underscore the importance of ecological aspects in understanding the evolution and maintenance of coloration in *T. brevispina* spiders.

Key words: color polymorphism; *Thelacantha brevispina*; genetic polymorphism; phenotypic plasticity; density; prey abundance; Moorea, French Polynesia

INTRODUCTION

Polymorphism is the occurrence of multiple discontinuous forms or morphs among individuals within an interbreeding population (O'Neill and Beard 2011). Visible polymorphisms, which can be readily observed and measured, have long been the focus of research in evolutionary biology to understand intraspecific variations (Huber and Hopf 2004). Examples of this widespread phenomenon include color and banding in the land snails (Jones et al. 1977), wing patterns in the butterflies (Baxter et al. 2008), and melanism in the peppered moth (Bishop and Cook 1980). The persistence of these polymorphisms over time suggests that they

carry adaptive functions thus are maintained by natural selection (Gillespie and Oxford 1998). Studying polymorphism and its adaptive values may be useful for examining the role of evolutionary processes in maintaining them and also the different modes of selection operating on different morph patterns.

Color and pattern may vary considerably among and within animal species. One striking example is color polymorphism, the occurrence of multiple discrete color variants within a population (Agrawal 2001). Such variation in color may be a direct reflection of differences among individuals as a consequence of genetic variation (i.e. genetic polymorphism) or may reflect a plasticity of

developmental processes in response to environmental conditions (i.e. phenotypic plasticity) experienced during ontogeny (Agrawal 2001, Hochkirch et al. 2008). It is worth noting that the existence of a plastic response to environmental cues may be genetically determined, therefore phenotypic plasticity is a complement rather than a contrast to genetic polymorphism (Hochkirch et al. 2008). Understanding how color polymorphisms are maintained and their adaptive function requires knowledge of how genetic and epigenetic environmental cues influence the development and phenotypic expression of organisms (Hochkirch et al. 2008).

Color polymorphism is a widespread phenomenon in spiders. Like many other arthropods, spiders display a broad range of colors and patterns that vary both inter- and intraspecifically (Oxford and Gillespie 2001). The majority of the display colors and patterns are genetically determined, thus resistant to environmental influences (Gillespie and Oxford 1998). The most spectacular example of such genetic polymorphism is found in the endemic Hawaiian happy-face spider, *Theridion grallator* (Theridiidae) with more than 20 opisthosomal (abdominal) color morphs described and maintained by balancing selection (Oxford and Gillespie 1996a,b). Though the coloration of many spiders is genetically fixed, color may change depending on specific environmental conditions. Such color changes are examples of phenotypic plasticity and can be passive (food-induced) or active (physiological, morphological, or behavioral) (Gillespie 1989, Gillespie and Oxford 1998). These changes vary between species and may be dependent on the ecology of the sex and different developmental stages (Gillespie and Oxford 1998). Phenotypic plasticity carries adaptive value as it enables rapid response to changing environmental conditions during ontogeny.

Thelacantha brevispina, the spiny-backed spider, is a color polymorphic orb-weaver in the family Araneidae and is native to India. Its

relative, the spiny-bellied orb-weavers of the genus *Gasteracantha* had been discussed in several reviews (Muma 1971, Gregory 1989). However, much less is known about the natural history and the basis of coloration in *T. brevispina*. Tropical islands like Moorea, French Polynesia offer an interesting opportunity to study and describe the biology of biodiversity, particularly arthropod diversity. *T. brevispina* spiders are invasive to Moorea and occur on the invasive coastal mangroves as well as the native *Hibiscus* trees. Characterizing the distribution and basis of coloration of *T. brevispina* on Moorea would provide a foundation for future investigations in predator-prey interactions, facilitation of co-occurring invasive species, and further ecological and evolutionary studies.

The first component of this study was to survey the occurrence of *T. brevispina* on Moorea and characterize their habitats. The second component investigated the relationship between spider density and prey abundance with respect to: (i) coastal vs. forest (habitat type), (ii) mangrove vs. *Hibiscus* (tree type). Spider density was hypothesized to be positively correlated with prey abundance, and both density and prey abundance would be higher in mangrove patches and coastal habitat. The final component of this study examined the basis of color variation in *T. brevispina*. Offspring produced by females of different, but known color morphs were split-brooded into two different habitats: coastal and forest *Hibiscus*. Siblings raised in different habitats were hypothesized to develop different colors as a result of environmentally induced developmental plasticity of coloration in *T. brevispina*. To complement the split-brood design, a laboratory reciprocal transplant was conducted with spiders at different developmental stages collected in the field. *T. brevispina* was hypothesized to change color in response to environmental cues associated with a particular habitat.

METHODS

Study site

The study was conducted along coastal and forest habitats on Moorea, French Polynesia from October 2012 to November 2012 (Fig. 1). 12 study sites were chosen based on presence of spiders. The first 3 sites were at the coastal mangroves, located near and in Haapiti (Fig. 1, Table 1: sites 1-3). All habitats consisted of mangrove aggregations with adjacent, more inland *Hibiscus* trees. *T. brevispina* spiders were easily seen between branches with high wind access. The next 3 coastal sites were at Opunohu bay, located in close proximity to the shrimp farm (Fig. 1, Table 1: sites 4-6). All habitats consisted of coastal *Hibiscus* trees with sparse branches and open space. Anthropogenic removal of *Hibiscus* branches observed in this area. The last 6 sites were inland forest habitats, located near the entrance to the Agricultural school and at Belvedere following the trail to the Belvedere overlook (Fig. 1, Table 1: sites 7-12). These forest habitats are characterized by high canopy cover with low wind access compared to coastal sites, and spiders were found high off the ground (>1m) between *Hibiscus* branches.

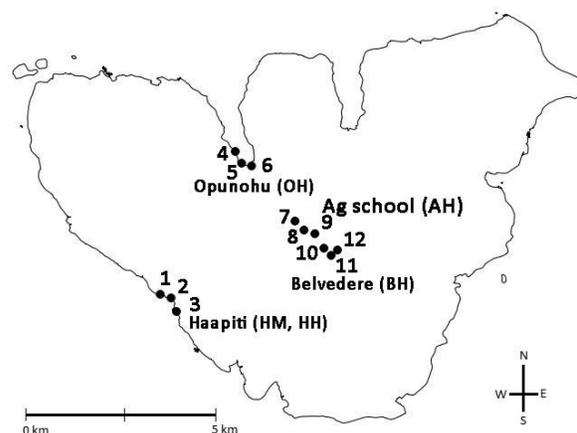


FIG. 1. Map depicting the locations of the 12 field sites sampled for *T. brevispina* spiders on Moorea. Numbers correspond to GPS coordinates and field site names on Table 1.

Study organism

As members of the Araneidae family, *T. brevispina* spiders rely heavily on their webs to capture prey. Webs are often found in open areas with high wind accessibility and are characterized by silk tufts found along the peripheral foundation lines. Webs are constructed at a slight angle from perpendicular to the ground, and spiders sit in the central hubs to await prey. Upon detection of prey, the spider immobilizes its prey through biting then carries the bitten prey

Table 1. List of GPS coordinates for each study site.

Site #	Longitude	Latitude	Site Name
1	149° 52' 37" S	17° 33' 19" W	Coastal Haapiti Mangroves (HM) and <i>Hibiscus</i> (HH)
2	149° 52' 26" S	17° 33' 23" W	HM & HH
3	149° 52' 20" S	17° 33' 37" W	HM & HH
4	149° 51' 17" S	17° 30' 48" W	Coastal Opunohu <i>Hibiscus</i> (OH)
5	149° 51' 11" S	17° 31' 00" W	OH
6	149° 51' 00" S	17° 31' 03" W	OH
7	149° 50' 15" S	17° 32' 01" W	Forest Agriculture school <i>Hibiscus</i> (AH)
8	149° 50' 05" S	17° 32' 11" W	AH
9	149° 49' 54" S	17° 32' 15" W	AH
10	149° 49' 44" S	17° 32' 30" W	Forest Belvedere <i>Hibiscus</i> (BH)
11	149° 49' 36" S	17° 32' 38" W	BH
12	149° 49' 29" S	17° 32' 32" W	BH

back to the central hub for consumption (Muma 1971). *T. brevispina* spiders appear to be immune to bee stings due to the protection of their hard carapace (Yoshida 1989).

T. brevispina spiders display a remarkable variation in color and pattern of the carapace. All spiders have two distinct white spots at the center of the carapace. Color patterns vary around the white spots with morphs ranging from white, orange, or brown markings to partial and complete black fill. Lighter morphs occurred along the coast in high wind area and low canopy coverage. In contrast, darker morphs were found in forest along trails with low wind access and high canopy coverage.

Captive rearing

15 females *T. brevispina* were maintained in the laboratory for egg laying at $28 \pm 1^\circ\text{C}$, moderate humidity, and 12h light:12h dark cycle. Each of the females was classified according to color morph and placed in individual plastic cups. The top of each cup was covered with 1.5x1.5 mm mesh to allow air flow and facilitate web building. Most females had eggs within 1-2 days post collection. Egg sacs were inspected on a daily basis for newly hatched spiderlings. On average, spiderlings emerged 7-9 days post-laying. Newly hatched spiderlings had two abdominal white spots but no coloration. After 2-3 weeks, color patterns began to develop and full color morph was achieved by the end of week 4. All spiders were fed on a diet of fruit flies and leafhoppers. Water droplets were given 3 times per week.

Presence/Absence survey

Survey data was obtained at different locations on Moorea during random visits. At each location, presence or absence of *T. brevispina* was recorded along with habitat characteristics: tree type, percent canopy cover (using a densiometer), tree density (branches/tree), and wind velocity (m/s). Habitat data was analyzed with ANOVA

using the statistical software JMP Version 10. Voucher specimens of spiders with different color morphs were collected, preserved in ethanol, and deposited into the Essig Museum of Entomology, University of California, Berkeley.

Density and prey abundance

To quantify *T. brevispina* spider density, six 15-meter transect plots were interspersed at each site. For sites 1-3, six transects were run each at mangrove and *Hibiscus* habitats. Along a transect line, all spiders were counted a meter out to left and right of the line (area of 30m²) with counts taken every meter. Active search was done for 30 seconds at each meter mark. Mangrove scaffold branches and *Hibiscus* lateral branches within the transect area were also recorded.

To assess prey abundance, six 6x8 inch sticky traps or fly papers were set out next to spider webs at each site (where transects were conducted) to estimate flying insect density per day. The size of each trap was similar to that of adult spider webs observed in the field. Not all insects found on traps would fall prey in the web. To estimate prey abundance, insects most often found in webs or observed to be commonly consumed by spiders during feeding time were identified and their numbers counted on the traps. Differences between density and prey abundance among habitats were analyzed using analysis of variance. Linear regression was run to analyze the relationship between density and prey abundance.

To estimate energy density, insects were collected (quantity matched the amount caught on the fly papers for each species per day), dried in a plant drying oven for 48 hours, and dry weights taken. The total reward or energy gain (E) by spiders was calculated with the following formula using the energy value (EV) of 22 J mg⁻¹ (Tewari and Kaushal 2007):

$$E = \# \text{ of insects} * \text{mean dry weight (mg)} * \text{EV}$$

The total energy gain was inferred from insect dry weights for both coastal and forest habitats to allow for a comparison.

Basis of coloration: split-brood

A split-brood design was used to investigate whether color patterns of *T. brevispina* spiders are influenced by different habitat conditions experienced during growth and development. Newly hatched spiderlings (N = 70) from 5 females with known color morphs from different sites were reared in two terrariums and fed on a biweekly basis. One terrarium with N = 35 (7 from each female) mimicked the coastal habitat with sparse *Hibiscus* branches. It was covered with thin mesh to prevent possible predation and exposed to the sun at the docks of the UC Berkeley Richard B. Gump Research Station. A fan was directed into the terrarium every morning around 07:30 (active feeding time observed in the field) for about 30 minutes to mimic windy conditions. The other terrarium, N = 35, was designed to be similar to forest habitat at the Agriculture school and Belvedere with high canopy density and low wind access. It was placed behind the Dirt Lab of the Gump Station under shade.

Basis of coloration: laboratory reciprocal transplant

A reciprocal transplant design was used to complement the split-brood experiment. *T. brevispina* spiders at different stages of development (juveniles and adults) were collected from coastal *Hibiscus* (N = 18) and

forest *Hibiscus* sites (N = 18). 9 individuals from coastal sites were transplanted to forest terrarium, and 9 remained in coastal terrarium as controls. Similarly, 9 individuals from forest habitat were transplanted to coastal environment and 9 were controls. The design was replicated 3 times with the same sample size and same duration of 8 days.

Quantifying color and estimating measurement repeatability

Color morphs of individuals from split-brood design were scored weekly once full color was achieved. Transplanted individuals were scored at the beginning and at the end of each replication event. Using IMAGE J, the abdominal area of each spider was selected and its mean RGB value determined. The mean RGB value measures the average darkness of the red, green, and blue channels from 0 (black) to 255 (white). Though green and blue colors are not found in *T. brevispina*, analysis using the red channel alone versus mean RGB proved to be similar (ANOVA, F = 12.4, p = 0.48). To standardize all images, each spider was taken with a color wheel background under the same lighting. The present scoring was performed blind with regard to the results of the previous scoring. To estimate measurement repeatability, 30 individuals were photographed and scored twice on the same day using mean RGB. The result was analyzed and showed no difference between the measurements (ANOVA, F = 21.5, p = 0.57). Color scores from the split-brood and transplant designs were both analyzed using ANOVA.

Table 2. Habitat characteristics at sites with and without spiders.

Site	Tree type	Ave % canopy cover	Ave tree density (branches/tree)	Ave wind velocity (m/s)
Spider	Hibiscus	48.3	54.5	0.66
No spider	Hibiscus	45	49.7	0.86
t-test		F = 0.26, p = 0.62	F = 0.98, p = 0.34	F = 1.97, p = 0.19

RESULTS

Presence/Absence survey

T. brevispina spiders were found in coastal and forest-type habitats on Moorea. Along the coast, spiders were observed at the stretch of mangroves and *Hibiscus* trees in Haapiti and the *Hibiscus* trees at Opunohu bay (next to shrimp farm) prior to reaching the Kellum Estate. In the forest, spiders were present on the *Hibiscus* adjacent to the Agriculture school, at the top of Three Pines, along the Three Coconuts trail, and along the way up to Mou'aputa and Mou'arotui. No spiders were found near the Gump Research Station, between the Kellum Estate and Gump, and along the way to Afareaitu.

Spiders were present on a variety of tree types, with the majority occurring on mangroves and *Hibiscus* trees. Habitat characteristics were analyzed for *Hibiscus* sites with and without spiders. There were no significant differences between sites in terms of percent canopy cover, tree density, and wind velocity (t-tests, Table 2).

Density and prey abundance: coastal vs. forest habitats

T. brevispina density and prey abundance were assessed and compared between different *Hibiscus* habitats. Spider density at the coastal sites was significantly higher than forest sites (ANOVA, $F = 5.99$, $p = 0.034$). However, prey availability was significantly

more abundant in the forest habitat (ANOVA, $F = 65.2$, $p < 0.001$). Spider density and prey abundance showed a negative relationship with lower prey count in areas of higher spider density (Fig. 2, linear regression, $R^2 = 0.56$, $p = 0.0014$). As prey abundance increases, spider density decreases quickly at first then gradually levels off at lower densities.

The most common insects caught on webs or consumed by spiders were those of the orders Hymenoptera (bees), Diptera (white-eyed flies), and Hemiptera (leafhoppers). Forest habitat had more flies and leafhoppers with flies made up the majority of the dry weights calculated, whereas the coastal habitat had a greater number of bees with much larger dry weight values. Using dry weights to infer energy density, coastal habitat yielded more than 2 times the energy density in the forest habitat (Table 3).

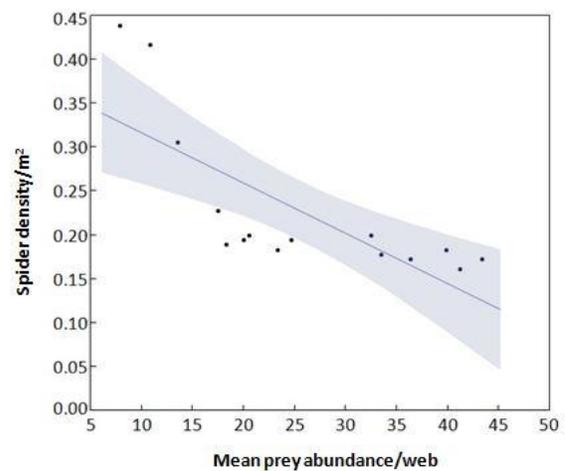


FIG. 2. Negative relationship between spider density and prey abundance.

Table 3. Inferred prey energy density using mean dry weights.

Order	# coastal insects	# forest insects	coastal mean dry weight (mg)	forest mean dry weight (mg)	inferred coastal E (kJ)	inferred forest E (kJ)
Hymenoptera	33.5	2	49	31	36.113	1.364
Diptera	235	459.5	1	1	5.17	10.109
Hemiptera	104.5	218.5	1	1	2.299	4.807
Total Reward (kJ)					43.582	16.28

Density and prey abundance: mangroves vs. Hibiscus trees

T. brevispina density and prey abundance were assessed and compared between different tree types at the coastal sites (sites 1-3). Spiders were found to be at higher density in the mangroves compared to *Hibiscus* trees (ANOVA, $F = 18.2$, $p = 0.013$). However, prey abundance was higher in the *Hibiscus* (ANOVA, $F = 19.3$, $p = 0.012$).

Basis of color variation: split-brood

The analysis of color variation in *T. brevispina* spiders that had been experimentally reared on coastal versus forest habitats showed no developmental plasticity of color in response to rearing environment. The color of the 70 offspring from 5 different color morphs showed strong resemblance to maternal color morph (Fig. 3, linear regression, $R^2 = 0.95$, $p < 0.0001$) but independent of rearing habitats (ANOVA, $F = 0.064$, $p = 0.80$). Offspring from one brood proved to be significantly different than those reared in other broods (ANOVA, $F = 340$, $p < 0.0001$; Tukey-Kramer test, $p < 0.05$).

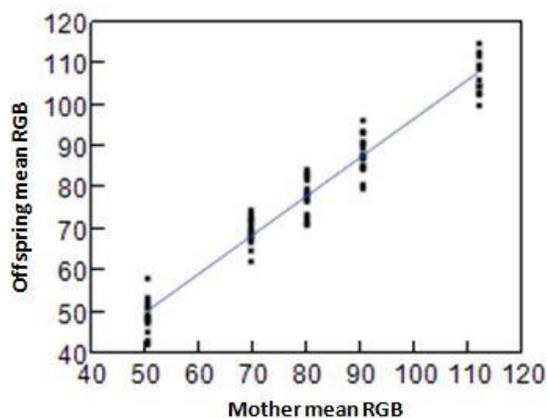


FIG. 3. Strong resemblance between mother color morph and offspring in a brood.

Basis of color variation: laboratory reciprocal transplant

The transplant experiment supported the lack of a plastic response in coloration of *T. brevispina* spiders of different age reared in different habitats. Transplanted spiders showed no significant change in color when comparing color pre- and post-transplants (Fig. 4, ANOVA, $F = 0.41$, $p = 0.74$). It is worth mentioning that the difference (final RGB – initial RGB) in offspring RGB in the 2 control and 2 treatment groups all moved up in the positive direction.

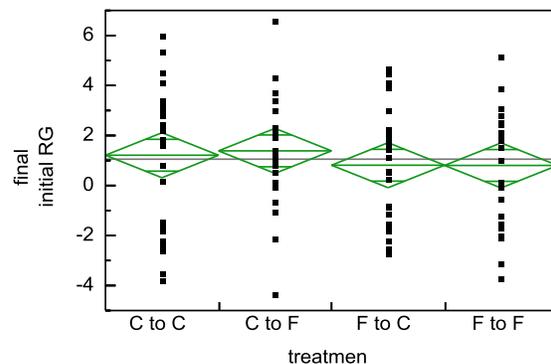


FIG. 4. No significant color changes pre- and post-transplant. C = Coastal, F = Forest.

DISCUSSION

Presence/Absence survey

Many aspects of *T. brevispina* biology remain unknown in the literature. The present survey documented the locations at which these spiders occurred on the island of Moorea. Though the survey was not exhaustive, general comments about the ecology of *T. brevispina* can be made. *T. brevispina* spiders were found on a variety of tree types and habitat conditions, suggesting that they are likely habitat generalists and can withstand variable environments. This finding agrees with studies done by Richardson and Hanks (2009) on 4 species of orb-weavers, all of which were generalists on a diverse grassland habitat.

Density and prey abundance: coastal vs. forest habitats

The present study showed that there were site differences in the statistically significant negative relationship between density of *T. brevispina* spiders and mean prey abundance. Coastal *Hibiscus* sites had higher spider densities supported by lower prey counts and vice versa for the forest *Hibiscus* sites. The finding contradicts the bottom-up view that population density could be regulated by prey availability (Trubl et al. 2012). The relationship between density and prey abundance did not follow a linear line, but leveled off at lower densities, similar to that of an exponential decay. Thus prey abundance may not be a good predictor of spider density and may be of lesser significance in relation to density (Bradley 1993).

Though less prey counts at the coastal sites to support higher density of spiders, prey sizes tended to be larger, especially the bees, thus providing a higher caloric value compared to the more abundant, smaller prey in the forest habitat. Hence the bottom-up view of population density could be regulated by prey energy density, with prey of higher caloric content supporting denser aggregations of spiders (Trubl et al. 2012). Another explanation for the negative relationship between density and prey abundance could be due to the high productivity in the coast compared to the forest. With more wind and air flow, coastal habitat has high insect turnover rate, thus provides for quick replacement of insect prey (Lopez-Medellin and Ezcurra 2012). It is worth noting that prey abundance was surveyed twice in the duration of the present study. These two events might have only captured a limited snapshot of the spatial and temporal variation in the coastal insect community.

Density and prey abundance: mangroves vs. Hibiscus trees

When comparing tree types, *T. brevispina* spiders occurred in higher density on coastal mangroves compared to the adjacent *Hibiscus* though there were more prey available on the *Hibiscus*. In the field, spiders were observed to be in dense aggregations in the mangroves where prey were present, but not necessarily with highest prey numbers. One possible explanation is that *T. brevispina* was controlling prey density since they were the only spider predator species occurring in the mangroves (Bradley 1993). Natural predators of *T. brevispina*, including birds, were not observed.

Another explanation for the high density of spiders in the mangroves could be related to general vegetation structures that mangroves provide, particularly for web building efficiency (Greenstone 1984). Mangrove trees have long narrow leaf blades connected radially from a central stem, providing a large open surface area to accommodate webs of various sizes and orientations. *Hibiscus* leaves tend to be round and larger, restricting the open surface area for wind accessibility, a major factor that contributes to prey capture success in these sit-and-wait predators as observed in the field. These results suggest that vegetation structure may be an important predictor of web-site selection for orb-weavers rather than prey abundance (Colebourn 1974, Greenstone 1984, Bradley 1993). Riechert and Gillespie (1986) reviewed the basis of web-site choice in 14 species of spiders in the order Araneae, and vegetation type was found to be important for 12 of these 14, while prey abundance was important for only 5 species.

Basis of color variation: split-brood

The lack of developmental plasticity in color variation in *T. brevispina* spiders that had been experimentally reared on different habitats suggests that a genetic origin of this trait is likely. There was a strong resemblance between the color of mothers and their offspring brought up from the same brood.

The split-brood design (of previously mated females collected in the field) did not allow for control of maternal environmental conditions or paternal contribution prior to egg laying that could have influenced development and coloration. All offspring from the same brood were fed the same diet of leafhoppers and flies, limiting the prey choices available that could affect the development of color in these spiders. The fact that these offspring were reared together could have allowed them to pick up on “likeness” color cues from other siblings, thus influenced their own coloration. The results of this study nevertheless conform to earlier studies of the Hawaiian happy-face spider *T. grallator* (Oxford and Gillespie 1996a,b) and the candy-strip spider *E. ovata* (Croucher et al. 2011, Oxford 1983), adding another case of likely genetic origin in color morph variation studied in spiders.

Offspring color also varied among broods, indicating site differences in coloration. In the field, lighter color morphs were observed along the coast whereas darker morphs were found in the forest habitat. This finding suggests the lack of gene flow or movement among different populations on the island. Spider distribution seemed to be random irrespective of habitat or background characteristics. At each location where spiders occurred, either light or dark morph predominated and such morph frequency could change abruptly moving to a different locality. This phenomenon is an example of area effects found in the land snail *Cepaea nemoralis* (Cain and Currey 1963). Area effects help explain the random distribution of color morph frequencies in *T. brevispina* on Moorea. Furthermore, such randomness could be the result of a founder event, in which a small number of individuals founded a new population at the loss of genetic variation (Agnarsson et al 2012). The unpredictable wind pattern on Moorea could have assisted the dispersal of spiders to found new populations around the island. Another possible explanation of color variations among sites is the different selective pressures

imposed at different sites. Spiders may try to blend in with their background to allow protection from possible predation or for more efficient prey capture. The reproductive biology of *T. brevispina* may contribute to the observed color variations.

Basis of color variation: reciprocal laboratory transplant

The transplant experiment confirmed that color variation in *T. brevispina* is likely to be genetic. The small changes in RGB measured pre- and post-transplant did not show a plastic response to rearing habitats. The mean differences of all the controls and treatments moved up in the positive direction, suggesting that spiders became lighter in color (larger RGB value) at the termination of the experiment. All spiders were photographed and measured under the same conditions and using the same methods. The measurement repeatability showed high reliability of the measurements. Thus the results of the transplant were not likely to have been influenced by measurement error or inconsistency. Perhaps the trend observed was due to insufficient sample size (N = 18 per replicate), duration of each replicate to allow for color change (8 days), or possibly stress-induced color change due to moving the spiders from their original habitats in the field.

Conclusions

The present findings do not support the hypothesis that coloration in *T. brevispina* spiders are influenced by developmental plasticity in response to rearing habitat experienced during growth. A genetic origin of color variation is likely given the strong maternal effect. Site differences in coloration could be the results of genetic drift or differential selective pressures in different habitats. Vegetation type or structure (not so much prey abundance) may influence site selection for web building and affect the ecology of *T. brevispina* species as a whole.

Further research in *T. brevispina* biology and ecology are necessary to understand the ecological and evolutionary aspects of their coloration.

As an invasive species on Moorea, *T. brevispina* spiders are considered to be pests. They occur on a variety of habitats from lowland coast to high altitude forests. They can effectively feed on many prey types, including high energy prey (e.g. bees) that are otherwise difficult to capture. They can withstand and thrive in high stress, windy environments that are inhabitable by other spiders. These characteristics of a generalist allow *T. brevispina* to spread around Moorea. It is speculated that these spiders could thrive as an invasive species due to their coloration. Therefore, understanding the evolution and maintenance of *T. brevispina* coloration requires further ecological ventures.

Future research

While this study attempted to understand *T. brevispina* coloration in relation to ecology, many aspects still remain unanswered and call for further exploration. Differential selective pressures from different habitats seemed to be an important factor in driving the distribution of color morphs and abundance of *T. brevispina* spiders. Investigating the habitat differences with respect to survival rates and movements of spiders may possibly explain the selective forces acting on coloration. In addition, a strong maternal effect was found within the same brood, suggesting high heritability between parent and offspring. Further investigation on parent-offspring heritability may reveal the extent in which genes control color polymorphisms in these spiders.

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