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Research Article

Effects of Habitat Change on the Web Characteristics and Fitness of the Giant Wood Spider (*Nephila pilipes*) in Sri Lanka

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We compare web properties and fitness of the Giant wood spider *Nephila pilpes* within and outside its natural rainforest habitat in Sri Lanka. The nonforest habitats comprised rural home gardens and plantations. We hypothesize that marked differences would be evident between the two habitats in (i) web properties and (ii) fitness of the female spiders. Web architectural and silk thread properties were measured in 25 webs of adult female spiders in each of the two habitats, while female abdomen size was used as the proxy for fitness. Findings support both hypotheses. The nonforest webs were more closely knit (smaller mesh spaces) and the hub was placed at higher position on the web than that in the forest webs both altering prey capture efficiency. Also, females in nonforest habitats were significantly smaller than those in the forest, indicating lowered fitness. The disparities in web characteristics and fitness are impressive given that the forest and nonforest habitats are located in close proximity, suggesting that rainforest orbweaver spiders such as *Nephila pilpes* may suffer population declines if the extents of natural forest continue to shrink.

1. Introduction

Loss and fragmentation of rainforests have led to serious implications on the survival of many species, often leading to population decline, or sometimes local extinction. Spiders are key inhabitants of rainforest ecosystems and, in ever changing tropical landscapes, their response to habitat change would be an important factor in deciding their fate. Web building spiders rely solely on their webs to entrap prey. Architectural and other properties of the web would therefore be expected to have a strong influence on the efficiency of prey capture. Limited evidence from captive studies has demonstrated that spiders alter web properties in response to changes in environmental conditions [1–5]. Some reported facts of interest are as follows: web size is influenced by the intensity of hunger such that starved spiders build larger webs than satiated spiders [6] microclimatic conditions around the web influence mesh size [5] properties of the silk thread vary with changes in prey availability [7–11]. Accordingly, we would expect habitat change, from forest to nonforest, to bring about changes in web properties of the rainforest spiders.

As web properties would have a direct bearing on the efficiency of prey capture, any change in web properties would in turn impact upon the fitness of the female spiders. Fitness of spiders under different habitat conditions has been assessed using the size of the females. Habitats of better quality would typically support larger females than poor quality habitats [12–14]. Here we would expect the fitness of rainforest spiders to be greater within forests than in the surrounding nonforest habitats.

The species selected for our study, carried out in Sri Lanka, is the Giant wood spider (*Nephila pilipes*), the largest of the orbweaver spiders in the country. It is a common inhabitant of the rainforest and is also seen in nearby areas outside the forest, in man-made, though nevertheless verdant, ecosystems such as rural home gardens and plantations. The aim of our study is to examine morphometric and web properties of the of the spiders in the natural forest in comparison with those in the man-made ecosystems in order to detect differences and, in particular, to test the hypotheses that (i) there would be some marked differences between the web properties of *N. pilipes* in the nonforest habitats compared to those in the forest and (ii) fitness of this species outside their natural habitat, i.e., in the nonforest areas would be lower than that within the forest. This is one of the few studies carried out *in situ* for investigating the effects of habitat change on a tropical spider species.

2. Methods

The forest habitats were located at the low and midelevation rainforests, Sinharaja and Kanneliya, both legally protected forest reserves, in the districts of Ratnapura and Galle. The nonforest habitats studied comprised a mosaic landscape, a mix of rural home gardens interspersed with rubber and small tea plantations, lying in close proximity (within 1 km) to the boundaries of the selected forests. A total of 50 intact webs, 25 each from forest and nonforest habitats, with resident adults of the Giant wood spider (*Nephila pilipes*), were used for the study. Individuals were identified as adults from their vibrant colour [15].

The spiders were gently removed from the webs and morphometric measurements were taken using a digital vernier caliper. Several web architectural characteristics that are important in determining the functional efficiency of an orb web were measured in the field. Measurements of the diameter (maximum horizontal span) and height (maximum vertical span) of the webs were taken and asymmetry determined using the formula web asymmetry index = 1- (d_h/d_v) where d_h is the diameter of the web, and d_v is the height [16]. A negative result would mean asymmetry with the vertical dimension being smaller than the horizontal dimension. The position of the hub on the web was also recorded. Hub asymmetry was determined using the formula hub asymmetry index = 1- (da/db) where da is the distance between the hub and the point on the edge of the web directly above it, and db the distance from the hub to the edge directly below it [16]. A positive value would mean asymmetry, with the hub being located above the centre of the web. Measurements were also taken of the web mesh space using the equation O_v-I_v/n-2 where, where O_v is the distance between the outermost spiral threads, I_v is the distance between the innermost spiral threads, and n is the number of vertical spirals following Prokop [17] and web incline angle determined using a trigonometric method. Additionally, strength of the silk threads were measured using a modified set up proposed by Bonino [18], and the thread diameter was measured using Electron Microscopic images (ZEISS EVO LS15 Scanning Electron Microscope, 500x magnification). Tensile strength (Newton per square meter (Nm^{-2})) of the threads was calculated by dividing the values for strength by the cross sectional area of the silk thread.

3. Results

Our first objective was to ascertain whether there were differences between the forest and nonforest habitats in web architectural and other properties of *N. pilpes*. Several notable differences were observed with respect to architectural properties of the web (Figure 1). One of the most striking differences was in the mesh space. Nonforest webs were considerably closer knit as evidenced by the significantly smaller mesh spaces than the forest webs (mean ± std. error (mm), Forest 0.42 ± 0.03; Nonforest 0.37 ± 0.02: F= 7.86, P<0.01) (Figure 1). In contrast to mesh space, although forest webs were slightly larger, web diameter did not differ significantly between forest and nonforest webs (mean ± std. error (cm), Forest 67.92 ± 3.73; Nonforest 62.90 ± 4.09; F= 0.82, P=0.37). In fact the difference in horizontal diameter between the webs in the two habitats (only about 5 cm) was small in comparison to the within-habitat variations observed (Figure 1). Vincent & Lailvaux [19] have indicated that web size is determined by the size of the spider, and may not therefore be affected by changes in the habitat. Hence we conducted a regression analysis using horizontal web diameter and female size (length of the abdomen). Our study showed that the relationship between these two variables was not significant for either the forest or nonforest habitats (Forest - web diameter = 53.45 + 0.55 abdomen length, F= 1.63, P=0.21, R^2 = 6.6 %; Nonforest - web diameter = 50.60 + 0.56 abdomen length, F= 0.67, P=0.42, R^2 = 2.8 %) (Figure 2). Web incline was nearly similar between forest and nonforest habitats (mean ± std. error (°) Forest 71.90 ± 5.17; Nonforest 68.90 ± 8.46; F = 2.34, p=0.13). (Figure 1).

For web shape, the negative values obtained indicate asymmetry, with the horizontal span being greater than the vertical span. The asymmetry was greater, although not significantly, in the nonforest webs (mean ± std. error, Forest - 0.09 ± 0.06; Nonforest 0.13 ± 0.04; F = 0.13, P =0.72) (Figure 3(a)). With regard to the hub position on the web, the positive values obtained show that the hub, and so the spider, is positioned above the central point of the web in both habitats. But, the significantly higher values obtained for the nonforest webs indicate that the spider is placed at a much higher position above the central point in nonforest webs in comparison to the forest webs (mean ± std. error, Forest 0.56 ± 0.02; Nonforest 0.67 ± 0.02; F= 11.64, P<0.01) (Figure 3(b)). Habitat-wise disparities were also observed for silk properties, tensile strength was higher (though not significantly) in the silk strands collected from forest webs when compared to those from the nonforest (mean ± std. error (Nm^{-2}), Forest 459 ± 72; Nonforest 396 ± 65.5; F = 0.43, P = 0.52), while the opposite was true for the diameter of the silk threads, where the values were greater in the nonforest webs (mean ± std. error (10^{-6} m), Forest 36.12 ± 5.39; Non - forest 43.65 ± 6.19; F= 0.84, P = 0.36), although this difference was also not statistically significant (Figure 4).

In assessing differences in fitness in forest and nonforest female spiders, comparison of means of the abdomen length shows that the spiders were considerably larger in the forest than in the nonforest habitats (mean ± std. error (mm), Forest 26.34 ± 8.40; Nonforest 21.55 ± 6.25; F= 5.22, P<0.05) (Figure 5).

4. Discussion

The present study shed light on some interesting changes that occur with respect to both web properties and fitness parameters of the Giant wood spider *Nephila pilpes* following the loss of their natural rainforest habitats and transformation

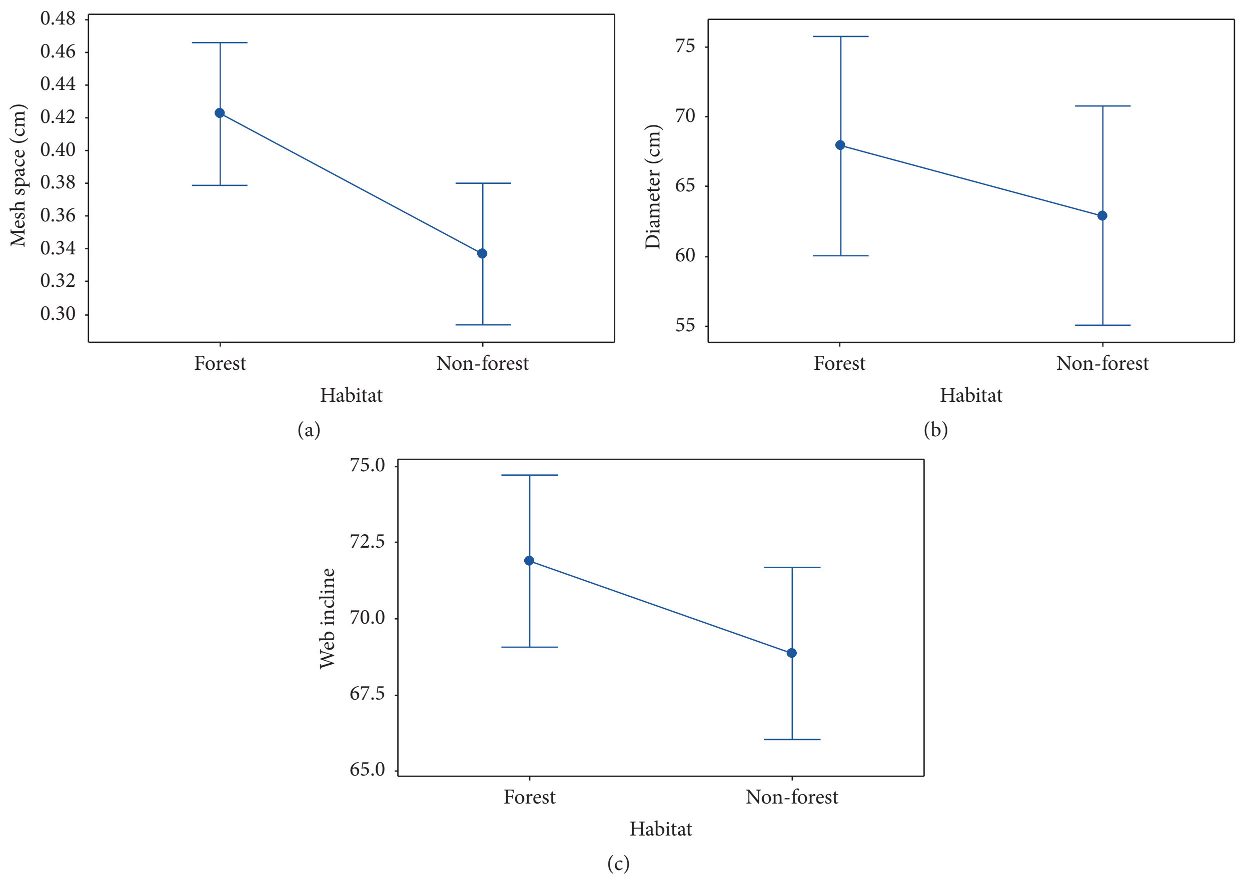

Figure 1: Web architectural properties (a) mesh size, (b) horizontal diameter, and (c) incline in *N. pilpes* inhabiting forest and nonforest habitats.

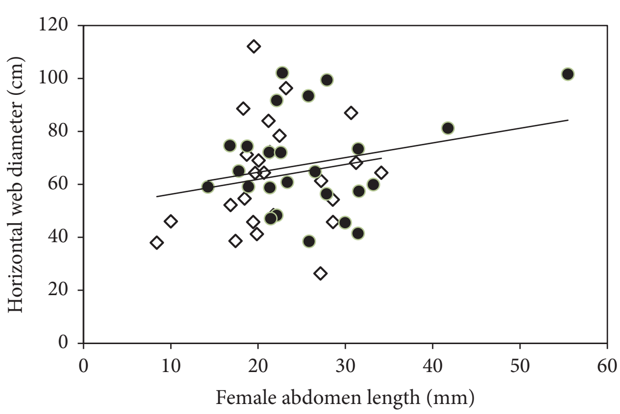

Figure 2: Relationship between abdomen size and web diameter in forest (solid circles) and nonforest (open diamonds) habitats in the wet zone of Sri Lanka.

of the areas concerned to man-made, though nevertheless verdant, ecosystems. Of the web properties studied, the mesh space (average distance between two spiral threads along a radial thread) was seen to be significantly smaller in the nonforest habitats compared to that in the forest webs. It was evident that forest habitats favored the construction of loosely woven webs (with considerably greater mesh space) while in the nonforest habitats mesh space was smaller and the webs more closely knit. Larger mesh spaces result in entrapping larger prey as established by Murakami [20]. Interestingly, several studies [21, 22] report that larger spiders with their webs having greater mesh space would capture and consume larger prey. Applying these speculations to the results obtained in the present study, the larger mesh spaces in the forest webs may result in the capture of larger and more profitable prey than those in the nonforest habitats.

A second significant result was in the different levels of asymmetry in the location of the hub in relation to the central point of the web. The positive values for hub asymmetry as recorded in the present study indicates that the hub is positioned in the upper part of the web, a character also seen in the other members of the subfamily Nephilinae [23]. One advantage of the hub being located in the upper part of the web is that, with the spider's large body size in comparison to other orb weavers, gravitational force would make its downward and lateral movement faster and easier than moving upward, when prey is trapped in the web [24, 25]. The differences in hub asymmetry between the two habitats were striking (forest 0.56, nonforest 0.65) suggesting that the spiders in nonforest habitats, poised at a greater height on the web, would be moving downwards towards the prey more often than would be the case in the forest habitats where the hub is located closer to the centre of the web.

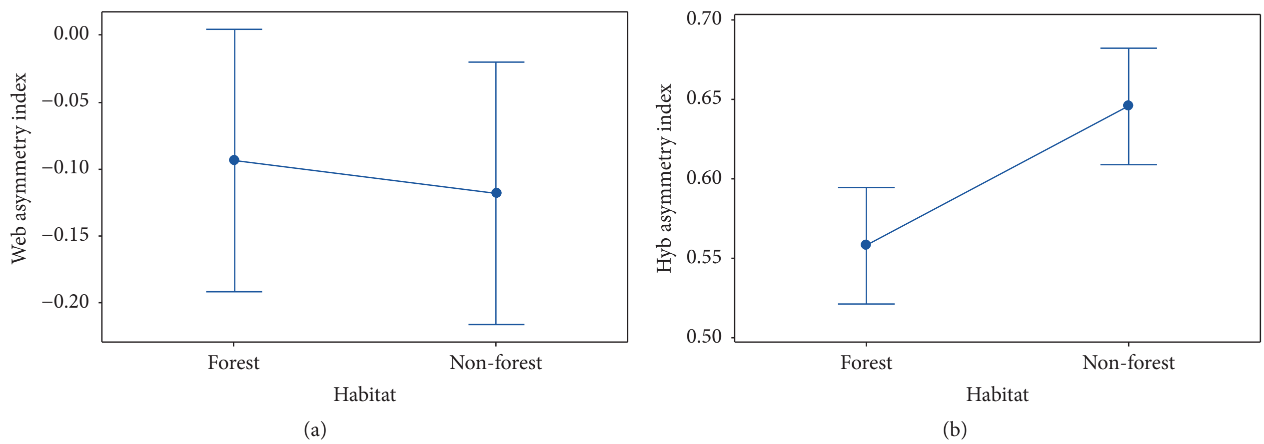

Figure 3: Variations in (a) web and (b) hub indices of symmetry in *N. pilpes* inhabiting forest and nonforest habitats.

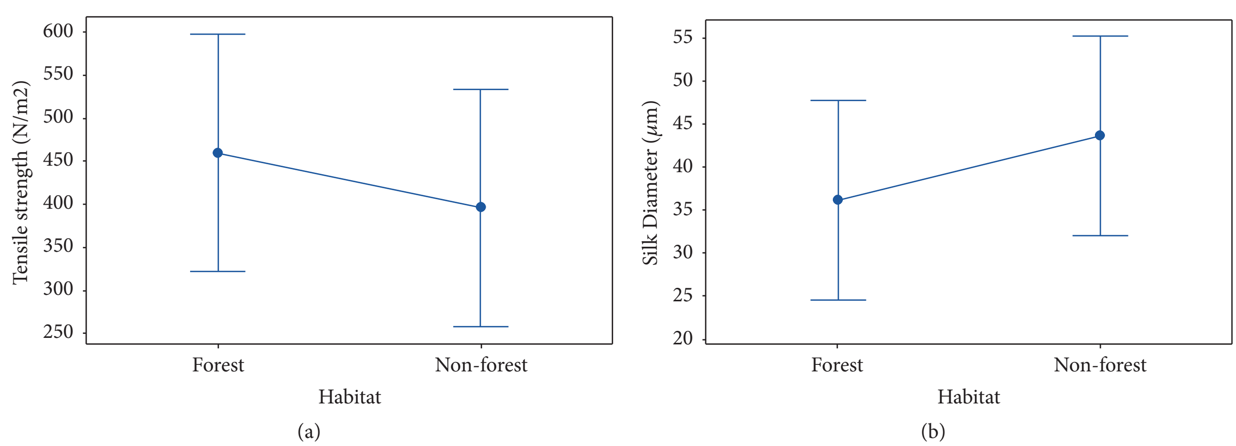

Figure 4: Variation in properties of silk thread (a) tensile strength and (b) diameter of silk thread in webs of *N. pilpes* found in forest and nonforest habitats.

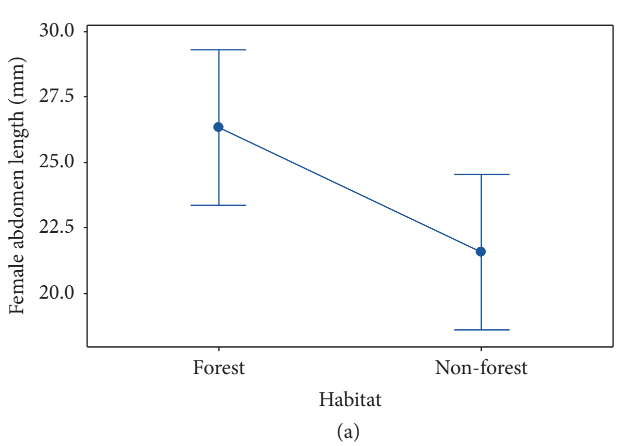

Figure 5: Variation in female abdomen size in *N. pilpes* occupying forest and nonforest habitats.

The two results on mesh space and hub position where there are significant differences between the webs in the forest and nonforest habitats provide positive evidence in support of the first hypothesis that there would be marked differences in the properties of the web between the two habitats studied.

One of the other web properties studied was web size. Although forest webs were slightly larger than those outside the forest, this disparity was small and insignificant in comparison to the differences in web size within each of the two habitats. Several explanations have been provided for variations in web size among individual spiders. It has been reported that spiders build smaller webs in wind exposed habitats thus reducing the possibility of breakage [5]. This could be a contributory factor in our study as the home gardens and cultivations were more exposed to wind due to reduced canopy cover than the forest habitats. Another interesting idea put forward with regard to web size by Foelix [6] and Sherman [26] relates web size to the intensity of hunger, with hungry spiders building larger webs than satisfied spiders. No evidence was obtained with regard to this in the present study, and neither did our study indicate any anatomical limitation in determining web size as predicted by Vincent & Lailvaux [19]. With regard to web incline, some ecologists have speculated that differences in web incline may influence the efficiency of prey capture [1] while others have stated that it is a species-specific trait [27]. No marked differences were evident in web incline between forest and nonforest webs in the present study.

Disparities in tensile strength and silk thread diameter were apparent between the webs in the forest and nonforest habitats although differences were not significant. The tensile strength of the forest webs was greater than that of the nonforest, while the reverse was true of the thickness (diameter) of the silk threads. As it has been shown that properties of the silk thread vary with changes in prey availability [7–11] the result in our study most likely indicates differences in the prey base in the two studied habitats. One can, however, only contemplate that the higher thickness of the silk fibres in nonforest webs might compensate somewhat for the loss of tensile strength in these webs.

Strong evidence was obtained in support of the second hypothesis set out in the present study. We proposed that changes in web properties would have some impact on the fitness of the female spiders and that females in the forest would be fitter than those in the nonforest habitats. Our results show that females in the forest were distinctly larger than those in the home gardens and plantations in the same geographical area. It is well known that morphological changes in animal species living in different environments are influenced by variations in food availability [28]. Hence, the larger size of the females in forest habitats must, at least in part, reflect the presence of a richer prey base in forest habitats in comparison to nonforest habitats, a fact that has been demonstrated elsewhere [29–32].

In the light of these findings what implications would forest loss have on the survival of the Giant Wood spider, a common inhabitant of the rainforest, in situations where the areas concerned are transformed into man-made ecosystems such as rural home gardens and plantations? Our results show that natural forest loss may result in marked changes in some of the properties of the orb webs with possible consequences on prey capture efficiency. The disparities observed in the other web features, although not statistically significant, are yet important, given that they occur in the forests and nonforest habitats that are located in the same geographical area and in close proximity to each other. We saw also that female spiders in the forest were larger and hence would be expected to produce a greater number of viable offspring than the smaller nonforest spiders. These trends suggest that rainforest orbweaver spiders such as *Nephila pilpes* may suffer serious population declines if the extents of natural forest continue to shrink.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Authors' Contributions

Tharaka Wijerathna, Mayuri R. Wijesinghe, and Inoka C. Perera designed the study. Tharaka Wijerathna and Dilini Tharanga conducted the data collection. Tharaka Wijerathna and Mayuri R. Wijesinghe compiled the manuscript. All authors read and approved the final version of the manuscript.

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