

Ecology and web allometry of *Clitaetra irenae*, an arboricolous African orb-weaving spider (Araneae, Araneoidea, Nephilidae)

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Abstract. Analysis of ecological data of the arboricolous nephilid spider *Clitaetra irenae* Kuntner 2006, endemic to Maputaland forests, South Africa, indicates the species' dependence on this highly threatened habitat. We tested *C. irenae* habitat dependence via GIS analysis by plotting the known distribution against southern African ecoregions. In the southern part of its range, *C. irenae* inhabits almost exclusively one ecoregion, the Maputaland coastal plain forests; but further north, in tropical southern Africa, it continues inland into Malawi's woodlands. We test and refute the hypotheses that *C. irenae* inhabits exclusively mature trees, trees of a particular species, trees with a smooth bark, tree habitats at certain height above ground, and only closed canopy forest stands. The ecological niche of *C. irenae* is flexible as long as suitable trees under at least partially closed canopy are available. We quantify the *C. irenae* ontogenetic web changes from orb to ladder and the simultaneous hub displacement towards the top frame. Such web allometry allows the web to increase vertically but not horizontally, which enables the spider to remain on the same tree throughout its development and thus the ladder web architecture is an adaptation to an arboricolous life style. Adult hub displacement, common in spiders with vertical webs, is explained by gravity. *Clitaetra irenae* web orientation on trees correlates with forest closure, and might indicate the Maputaland forest quality. We argue for utilization of the ecology of arboricolous nephilid orb-weaving spiders (*Clitaetra* and *Herennia*) in systematic conservation assessments in the Old World tropics.

Keywords: Behavioral ecology, evolution, conservation, Maputaland, South Africa, *Herennia*

Opsomming. Analise van ekologiese data van die boombewonende nephilid spinnekop *Clitaetra irenae* Kuntner 2006, endemies tot Maputaland woude in Suid-Afrika, dui die spesie se afhanklikheid van hierdie hoogs bedreigde habitat aan. Ons het *C. irenae* habitat afhanklikheid via GIS analiese getoets deur die bekende verspreiding teen die suider-Afrikaanse ekologiese streke aan te teken. In die suidelike deel van die verspreiding kom *C. irenae* in slegs een ekostreek, die Maputaland kusvlakke woude, voor, maar verder noord in die verspreiding kom dit verder in die binneland, in Malawiese bosveld, voor. Ons toets en verwerp die hipotesisse dat *C. irenae* slegs volgroeide bome bewoon, bome van 'n spesifieke spesie, bome met gladde bas, boomhabitate op 'n sekere hoogte van die grond af, en slegs toe kroonbedekking woude. Die ekologiese nis van *C. irenae* is aanpasbaar solank daar geskikte bome onder ten minste gedeeltelike toe kroonbedekking beskikbaar is. Ons kwantifiseer *C. irenae* ontogenetiese webveranderings van 'n wawiel- na 'n leerweb en die gelyktydige verskuiwing van die kern na die bokant van die raam. Sulke web allometrie gee die spinnekop die vermoë om die web vertikaal te vergroot sonder horisontale veranderinge, wat die spinnekop in staat stel om op dieselfde boom te bly regdeur sy ontwikkeling. Ons sien die leerweb dus as 'n aanpassing tot boomlewende gewoontes. Volwasse kern verskuiwing, algemeen in spinnekoppe met vertikale webbe, word deur gravitasie verduidelik. *C. irenae* se web oriëntasie op bome korreleer met kroonbedekking, en kan 'n aanduiding wees van Maputaland woud kwaliteit. Ons stel voor dat nephilid wawiel-web spinnekoppe (*Clitaetra* en *Herennia*) se ekologie gebruik word in sistematiese bewarings assesserings in die Ou Wêreld tropiese gebiede.

Identifying areas of high conservation value (systematic conservation assessment sensu Knight et al. 2006) is one of the main priorities of modern ecology and conservation biology. Traditionally, conservation assessments have been largely based on vertebrate biodiversity data, while data on more diverse groups such as arthropods remain poorly utilized. This is particularly true for species-rich tropical faunas, where the natural history and ecology of most arthropod species continue to be unstudied. Among spiders, a clade with nearly 40,000 described species (Platnick 2007) and many more projected (Coddington & Levi 1991; Coddington 2005), potential indicator species are rarely identified. Most recent studies have investigated the impacts of pollution, disturbance,

and habitat classification on spiders at the community level, while species-level studies have focused on effects on predation ecology and heavy metal assimilation (Marc et al. 1999). However, these studies primarily dealt with the European and American faunas, while examples from the Afrotropical region are unknown. Here, we investigate the ecology of the recently described *Clitaetra irenae* Kuntner 2006, an arboricolous nephilid spider endemic to southern African forests, and use the newly acquired behavioral and ecological data to test its dependence on a highly threatened habitat – the Maputaland coastal plain forests.

Maputaland is an ecological-geographical entity comprising the coastal plain of north-eastern parts of KwaZulu-Natal (South Africa) from Richards Bay (28°48'S, 32°05'E) in the south to Xai-Xai in southern Mozambique (25°02'S, 34°25'E)

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in the north, and extending inland along the Lebombo Mountain range into eastern Swaziland (Olson et al. 2001; Van Wyk & Smith 2001). Due to the high levels of plant and vertebrate endemism (Van Wyk 1994, 1996; Van Wyk & Smith 2001) and the patchy distribution of unique habitats such as sand forest, Maputaland is of prime conservation importance. Furthermore, the composition of certain faunal and floral assemblages of different sand forest patches are significantly different (e.g., Kirkwood & Midgley 1999; Matthews et al. 1999, 2001; Van Rensburg et al. 1999, 2000), which supports the conservation of this particular habitat and its accompanying biological diversity throughout the region. Maputaland appears among six out of nine global biodiversity conservation priority areas (Brooks et al. 2006), being recovered within the crisis ecoregions, the biodiversity hot spots, the endemic bird areas, the centers of plant diversity, and the global 200 ecoregions, as well as within a megadiverse country, South Africa (for details see Brooks et al. 2006, and references therein).

The Old World tropical nephilid spider genus *Clitaetra* Simon 1889 is important in araneoid systematics because of its phylogenetic position as the sister taxon to all other nephilids (Kuntner 2005, 2006); these, in turn, appear to be the basal araneoid lineage (Kuntner et al. 2008). While the large-bodied nephilids (*Nephila*, *Nephilengys*) are well studied (Kuntner 2007) and recognized as ecologically important in most (sub)tropical ecosystems, *Clitaetra* ecology has largely been unknown (but, see Kuntner 2006). Of the six known *Clitaetra* species only *C. irenae* (Fig. 1) biology has been studied in some detail—Kuntner (2006) focused on its web-building behavior and general natural history. *Clitaetra irenae* was found in South Africa's subtropical coastal dune and sand forests of northern KwaZulu-Natal, with an outlying museum record from Malawi (Kuntner 2006: fig. 26). As in the Australasian nephilid spider genus *Herennia* Thorell 1877 (see Kuntner 2005), *Clitaetra* species are obligate tree dwellers building orb-webs against tree bark (Figs. 1, 2), with a few centimeters clearance between the planar web and the substrate. As in *Herennia* (Kuntner 2005), *Nephilengys* Koch 1872 (Japyassu & Ades 1998; Kuntner 2007), and *Nephila* Leach 1815 (Bleher 2000), juvenile *Clitaetra* webs resemble standard araneoid orb-webs (Figs. 2D, E). However, the webs of adult female *C. irenae* are highly modified *ladder webs* (Figs. 2A, C), defined as two dimensional orb-webs with parallel side frames and zig-zag sticky lines substituted for spirals (Kuntner et al. 2008:fig. 23). The species' apparent dependence on a particular habitat (Maputaland forests) and microhabitat (mature trees), as indicated by historical distribution records and the distribution of these particular forests, prompted our detailed investigation into its behavioral ecology emphasizing its ontogenetic web architecture shifts.

We investigate *C. irenae* web allometry by quantifying the developmental modification of the orb web into a ladder, pose a behavioral explanation for such an allometric shift, and deduce its ecological implications. Through explicit hypotheses (below) we examined whether or not the web modification in *C. irenae* correlates with a particular habitat type, with climatic conditions and/or altitude, and whether the species depends on mature Maputaland forests for sustainable populations. A species that is a narrow endemic of southern

Africa and a narrow habitat specialist (an obligate tree dweller) in a threatened coastal plain habitat is potentially at risk of habitat loss, and could be added to the list of species used as indicators of habitat quality.

Specifically, we tested the following hypotheses:

- (1) *Endemism*: Kuntner (2006) suggested that *C. irenae* was endemic to northern KwaZulu-Natal. However, such an hypothesis was defined geographically, not ecologically, and failed to explain the single outlying record from Malawi (Kuntner 2006). We tested whether *C. irenae* is endemic to the wider Maputaland (including Mozambique and Swaziland) by using precisely defined ecoregions (Olson et al. 2001).
- (2) *Habitat preference*: Most material examined by Kuntner (2006) was collected in sand forests along the Maputaland coastal plain. We investigated Kuntner's (2006) expectation that *C. irenae* is confined to mature sand forests. During our survey we noted the habitat type and canopy closure.
- (3) *Tree preference*: To test the spiders' dependence on a particular tree species we attempted to identify all trees where spiders were found. We predicted the spiders would prefer a particular tree species as vaguely suggested by Kuntner (2006).
- (4) *Tree size*: If the species was confined to mature forests, we predicted that larger spiders would prefer larger trees, and that web size would correlate with spider size.
- (5) *Substrate (bark) structure*: To test if the spiders utilize certain types of substrate, we classified bark into three categories (smooth, medium, or rough). We expected that trees with smooth bark would be more likely to host these spiders as the uneven surface of rough bark may hinder two-dimensional web construction.
- (6) *Website orientation*: The spider's website orientation on a tree might differ between closed canopy forests and partially open canopy tree stands (woodland/thicket) due to sunlight penetration. Assuming that the species is indeed native to closed canopy forests and that inhabiting other types of tree stands is an artifact of habitat fragmentation, we expected that we would find no web orientation preference in closed canopy stands, where continuous direct sunlight is an exception. In contrast, in more open tree stands where webs could potentially be exposed to direct sunlight, web orientation should be away from the sun (to the south).
- (7) *Distance from ground*: Finally, we tested for differences in web height above ground among the spider instars (size classes). We predicted that spiders would preferentially occupy lower positions on a tree as they age because larger tree trunk circumference closer to the ground would be more suitable for larger webs.

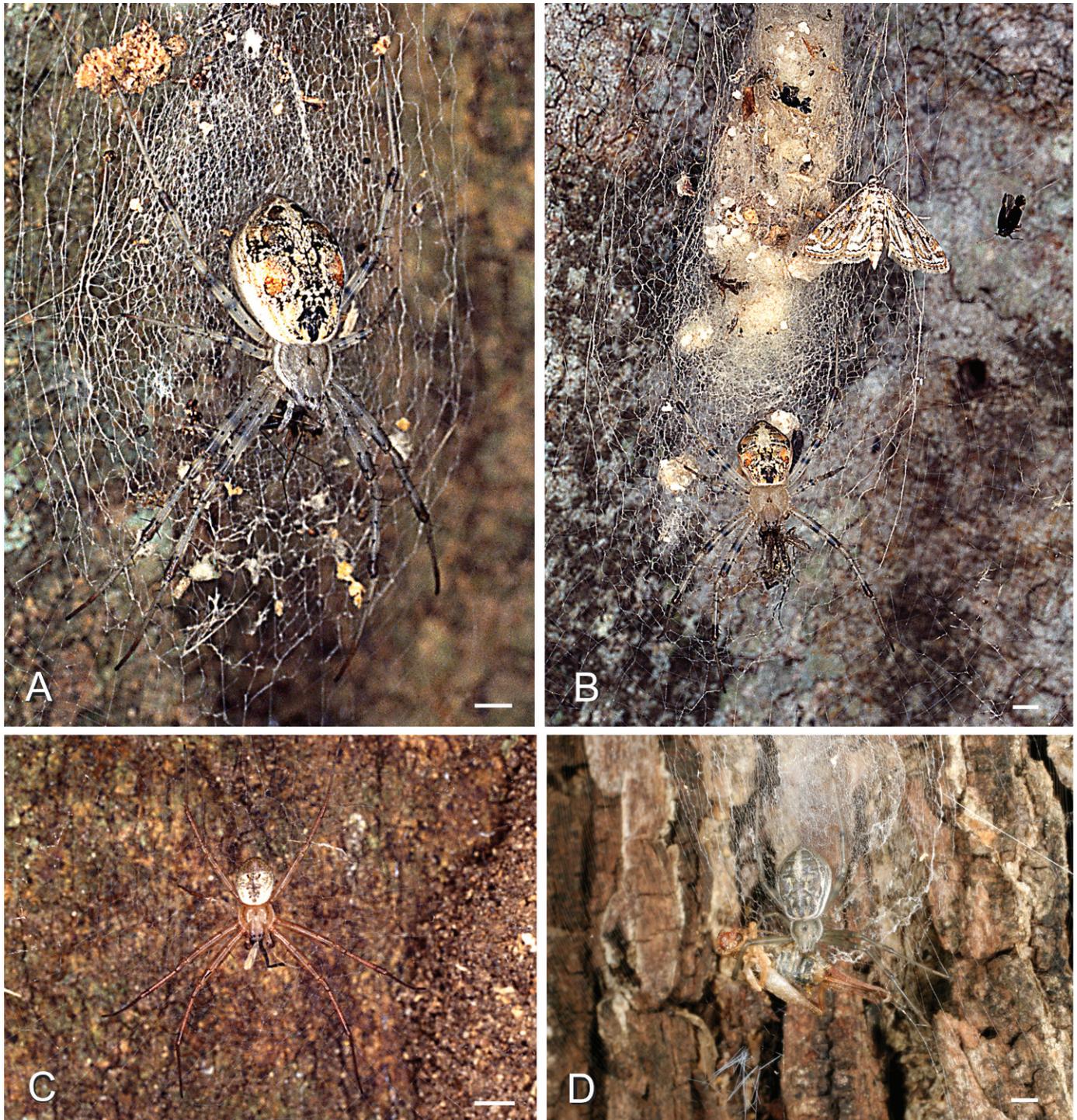


Figure 1.—*Clitaetra irenae* from South Africa (A–C, Fannies Island, 2001; D, Ndumo Game Reserve, 2006): A. Female holotype (see Kuntner 2006) at the hub of her web; B. Female feeding at the hub of her web; note the egg-cases above the hub camouflaged with prey remains; a male was present in her web (not shown); C. Paratype male (see Kuntner 2006) at the hub of his orb web, feeding on dipteran prey; D. Subadult female at web hub, feeding on cricket. Scale bars = 1.0 mm.

- (8) *Web allometry*: *Clitaetra irenae* web architecture shifts during spider ontogeny from orb to ladder web. Thus, we predicted that the *ladder index* and the *hub displacement index* (both defined below) would increase with spider size.

METHODS

Field study.—We visited six reserves (Fig. 3) in KwaZulu-Natal (South Africa) between 9–30 April 2006, the period when adult *Clitaetra irenae* are known to occur (Kuntner 2006). These reserves (Ndumo Game Reserve, Tembe Ele-

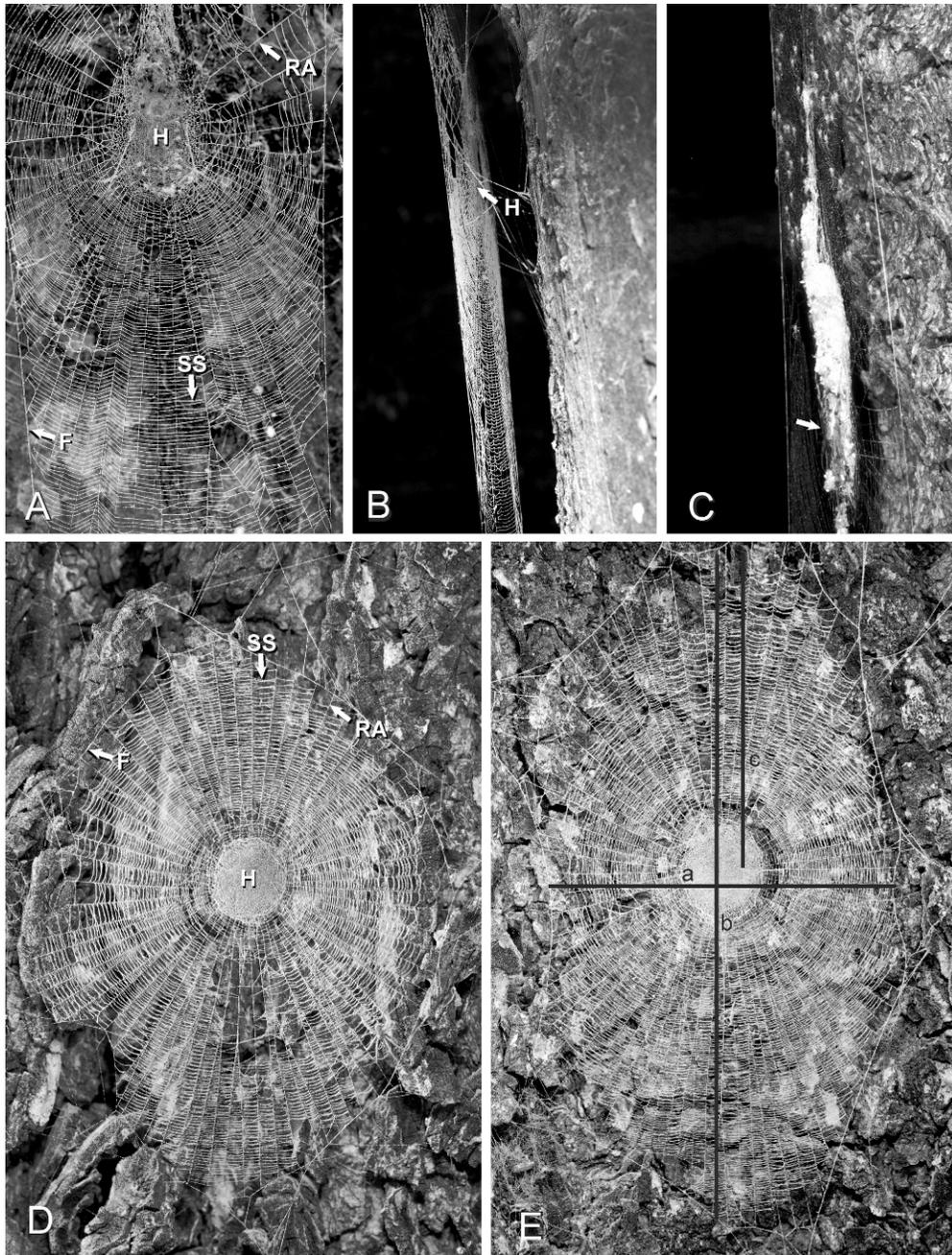


Figure 2.—*Clitaetra irenae* web architecture: A–C. Adult female webs; A. Frontal view, note ladder shape of web with parallel side frames (F), “sticky spiral” (SS) not spiralling, with silk enforced hub (H) displaced towards top frame; B. same web, lateral view; C. Female (arrow) in web, with first instar offspring in upper web; above hub is empty egg sac. D. Juvenile web (second instar); note typical orb-web architecture with bent side frames (F), round sticky spiral (SS), and upper radii as long as lower ones. E. Another second instar web, with parameters measured (a = web width, b = web height, c = top frame to hub). Photographs by M. Kuntner taken in Ndumo Game Reserve, South Africa, 2006; web measurements (cm) in A, B: a = 8, b = 29, c = 10.5; D: a = 5, b = 11, c = 5.5.

phant Park, Kosi Bay Nature Reserve, Sodwana Bay National Park, Hluhluwe-Imfolozi National Park, and the Greater St. Lucia Wetlands Park) slightly surpass the previously known *C. irenae* geographic range, except for the Malawi datum (Kuntner 2006), and therefore test the species’ geographical limits in Maputaland. Within the reserves we searched for the easily recognizable species (females, see Fig. 1A; males, see

Fig. 1C; for identification details see Kuntner 2006) at various localities, focusing on all available habitat types.

Where more than a single *C. irenae* spider was found, we measured the following ecological and behavioral parameters on all webs: date of collection; locality; site; habitat; latitude and longitude; host tree species (if known); tree bark structure categorized as smooth (as exemplified by *Celtis africana*),

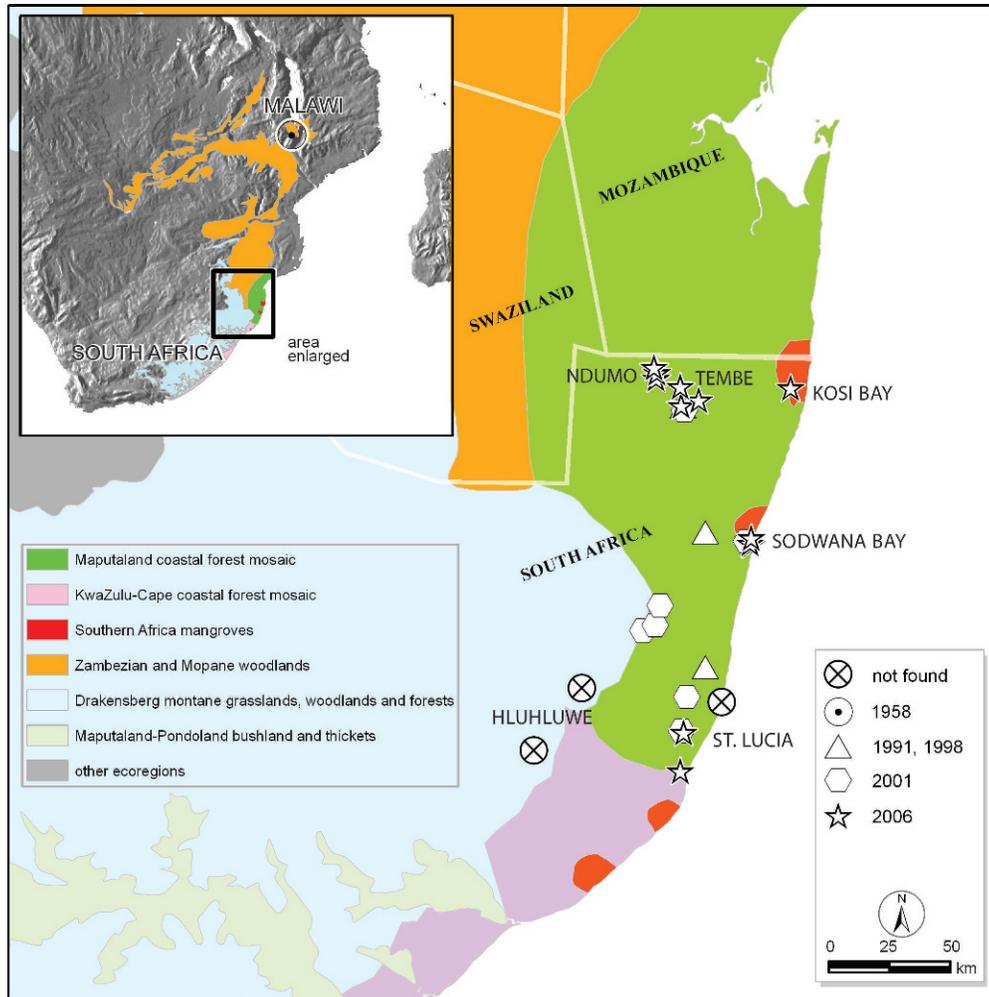


Figure 3.—*Clitaetra irenae*, currently known distribution plotted against southern African ecoregions. The outlying 1958 Malawi record (see Kuntner 2006) falls into “Zambezan and Mopane woodlands,” which stretches south adjacent to “Maputaland coastal forest,” the species’ prime ecoregion. The 1991–2001 data are from Kuntner (2006), new field records (2006) are from this study.

medium (as in *Balanites maughamii*), or rough (as in *Acacia nigrescens*); tree trunk circumference at the level of spider web hubs; canopy coverage categorized as closed, partially open, or open; stage or instar number; web width (Fig. 2E), web height (Fig. 2E), distance from web hub to top frame (Figs. 2D, E) and web hub height above ground; website orientation (8 directions: N, NE, E, SE, etc.), and possible further comments.

The first six (autecological) parameters document locality, habitat, and test hypothesis 2 (habitat preference). The next four parameters, i.e., host tree species, bark structure, trunk circumference and canopy coverage, are microhabitat data and test hypotheses 2–5. Spiders were assigned to seven categorical size classes (stages) corresponding to ontogenetic instar numbers (size correlates with age and instar number). Instar numbers were estimated from relative spider size, falling into fairly discrete size classes, assuming seven post-egg sac instars during female ontogeny: adult females were scored as 7, newly hatched animals 1, and others fell in between up to 6

(penultimate). Instars 2–7 build their own webs, but first instar spiderlings remain in the mother’s web (Fig. 2C). No developmental study has been done on *Clitaetra*. The assumption of seven instars in *C. irenae* ontogeny follows from data on other nephilids; e.g., the giant females *Nephila pilipes* (Fabricius 1793) go through about 10 juvenile instars while the small males go through about 4, the number of molts depending on the season and food availability (Higgins 2002). Three web parameters, namely web width, web height, and distance from hub to top frame, quantified developmental shifts in webs (see below). The last two parameters, distance from hub to ground and website orientation, indicate microhabitat preference and test hypotheses 6 and 7.

In order to increase visual contrast, webs were dusted with cornstarch for measurement and photography. All measurements were taken with a tape measure and are reported in centimeters, unless noted otherwise. Web orientation was taken with a compass. Web architecture abbreviations are: H = hub (Figs. 2A, B, D, E); F = frame (Figs. 2A, D); RA =

radius (Figs. 2A, D); SS = sticky spiral (Figs. 2A, D); a = web width (Fig. 2E); b = web height (Fig. 2E); c = upper web height = distance top frame to hub (Fig. 2E).

Web allometry.—We derived two ratios quantifying web allometry. The *ladder index* is the relative web height, defined as the ratio of web height to web width, and quantifies the transition from orb to ladder web during ontogeny. Similar to web shape sensu Zschokke (1993), the ladder index, as used here, differs in values increasing with extreme architecture. *Hub displacement* is lower orb/total web height using the formula $(b-c)/b$, where b = web height and c = top to hub (Fig. 2E). Hub displacement index is similar to web asymmetry indices of Masters & Moffat (1983), Rhisiart & Vollrath (1994), and Kuntner et al. (2008), but its values increase rather than decrease with the hub being eccentric towards the top web frame.

Statistical analyses.—We explored the relationships between the spider size (instar) and the following variables: 1) web height, 2) web width, 3) distance of web from the ground, 4) tree circumference, 5) ladder index, and 6) hub displacement index. Web parameters were plotted as box-plots (Tukey 1977). Due to the low number of webs in stages 4 and 5, individual points were plotted for these stages. Differences in medians between stages 2 and 7 were tested using the Mann-Whitney *U*-test. Freely available statistical environment R (R Development Core Team 2006) was used for plotting and for significance tests. Web orientation on trees (eight main directions) was interpreted through circular statistics using the Rayleigh test (Fisher 1993).

GIS analysis.—In order to test hypothesis 1 (endemism), we analyzed all available *C. irenae* locality data (Kuntner 2006; this study) using GIS. Our analysis builds on the digital base map by Bletter et al. (2004), which was obtained from the New York Botanical Garden (http://www.nybg.org/bsci/digital_maps/), with permission from the authors. The base map, which derives from the Environmental Systems Research Institute (ESRI) data sets ArcWorld®, ArcAtlas®, and Digital Chart of the World® (<http://www.esri.com/>), was built specifically for the Neotropics (Bletter et al. 2004), but also contains detailed data on the World's terrestrial ecoregions (Olson et al. 2001), courtesy of the World Wildlife Fund (<http://www.wwf.org/>). Olson et al. (2001) recognize 867 terrestrial ecoregions worldwide, which is a much improved resolution compared with previous attempts to classify terrestrial biotas. The map delimits six ecoregions within the geographical limits relevant to this study (Fig. 3). The *C. irenae* locality data (1958; 1991–2001 data are from Kuntner (2006); new field records (2006) are from this study) were superimposed on the southern African part of the base map using ArcView® GIS.

RESULTS

Clitaetra irenae occurred in all reserves (Fig. 3) except Hluhluwe-Imfolozi National Park, which falls into the Drakensberg montane grasslands, woodlands, and forests ecoregion (Fig. 3). In Kosi Bay and Sodwana Bay the spiders were present but their abundances per trees were too low to be measured. In some reserves, e.g., Ndumo and Tembe, the species was abundant. The outlying record of a single *C. irenae* male from Malawi (1958 datum from Kuntner 2006) falls on

the ecoregion “Zambezi and Mopane woodlands,” which stretches south adjacent to “Maputaland coastal forest” (Fig. 3), the species' main ecoregion.

Figure 4 summarizes the data obtained in Ndumo Game Reserve, Tembe Elephant Park and the two localities in the Greater St. Lucia Wetlands Park. The full data set with exact geographical coordinates for each habitat within the reserves is published online at www.nephilidae.com. In total, we investigated 166 spiders and their webs, the majority ($N = 118$, 71%) being second instars; the numbers of other instars investigated were much lower (Fig. 4A). Habitat preference characterizes the four forest types where the webs were measured (Fig. 4B). We characterized the habitat at Nyamiti Hide (Ndumo Game Reserve), where the majority of the aggregated second instar webs were found, as “riverine bush” (“deciduous orthophyll scrub with trees” of De Moor et al. (1977); “subtropical bush” of Haddad et al. (2006)), since the tree stands had a partially open canopy, with the terrain sloping gradually towards the Nyamiti Pan. Fig. 4C show that the most data (133 individuals) were taken in forest stands with only partially open canopy (riverine bush at Nyamiti Hide was all partially open habitat), and that all sand forest patches examined (Ndumo, Tembe, St. Lucia) were closed canopy (33 data points). There was little overlap of tree species (if known) between localities. However, sand forest trees harboring spider webs had a smooth and medium bark texture, while those in riverine bush had rough or medium bark (Fig. 4D).

Figures 5A–F show the relationships of interval and ratio data by instar, and report the results of the non-parametric comparisons (Mann-Whitney *U* test) of instar 2 ($n = 118$) and 7 ($n = 18$). Web height and web width increased significantly with spider size (Figs. 5A, B, $P < 0.001$). These two relationships support our assumption that spider web size correlates with age (instar). No significant differences were found in the web distance from the ground (Fig. 5C, $P = 0.39$) among the spiders of different size. Contrary to our prediction, larger spiders did not prefer larger trees (Fig. 5D, $P = 0.15$). However, as predicted, both measures of web allometry, i.e., the ladder index (Fig. 5E, $P < 0.001$) and the hub displacement index (Fig. 5F, $P < 0.001$), increased with spider size.

Figure 6 plots web orientation frequencies in eight categories (north, northeast, east, etc.) using circular statistics (Fisher 1993). Pooling all data (Fig. 6A) shows that *C. irenae* webs were randomly distributed on all sides of trees. However, the closed canopy data (Fig. 6B) reveal a significant (Rayleigh test, $P < 0.05$) preference for the northern side of trees, and the partially open canopy data (Fig. 6C) plots as significantly bimodal (Rayleigh test, $P < 0.05$), the spiders preferring southern and eastern faces of trees. Similarly, we found that the webs on smooth bark (only found in closed canopy sand forests), showed a significant preference towards the north. However, the webs on medium bark (closed and partially open forests), and on rough bark (only in partially open canopy forest), showed random distributions. The northern orientation of webs under closed canopy is related to canopy closure, not bark type, as both subsets of webs, the smooth bark webs and medium bark webs showed a significant preference for the northern side of trees (Rayleigh test, $P < 0.05$ and $P < 0.1$, respectively).

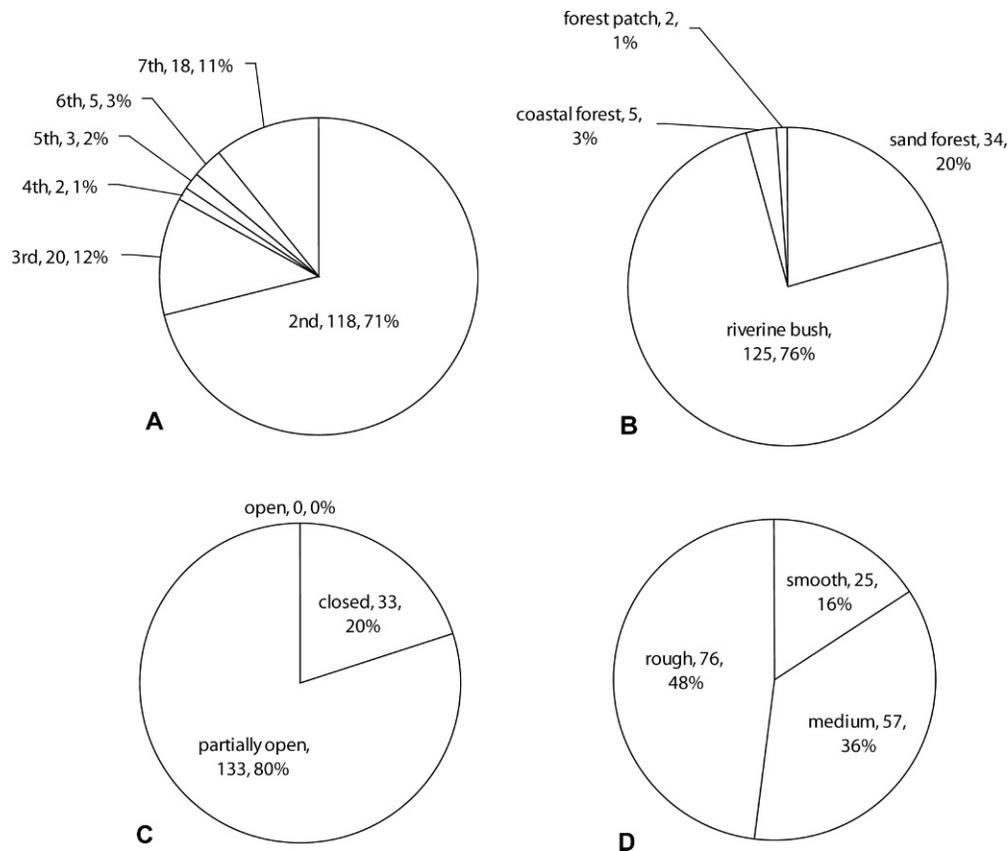


Figure 4.—Field data summary (category, *n*, percentage): A. Individuals by instar; B. Habitat; C. Canopy coverage; D. Bark structure.

DISCUSSION

The disproportionately high numbers of small juveniles (instar 2) measured compared to other instars (Fig. 4A) may be explained by the fact that second instars tend to aggregate around the mother's web and are thus more easily located than instars 3–6. One of the alternative explanations, the higher mortality of larger juveniles, is contradicted by the fact that 18 females versus fewer 4–6th instar juveniles were collected (Fig. 4A). Seasonality seems the best explanation: as our study focused on the known adult *C. irenae* phenology, our April field work only sampled a part of the species' life cycle.

Distribution and phenology.—The ecoregion with the majority of *C. irenae* records (Fig. 3) is the Maputaland coastal forest mosaic, but some records also fall into the adjacent ecoregions, including the Southern Africa mangroves and the KwaZulu-Cape coastal forest mosaic. The localities we visited that fall into these latter two ecoregions were no different with regards to forest structure and tree and bark microhabitat from the ones falling into Maputaland, and thus we view these records as continuous with “larger Maputaland.” At this resolution, the borders between these ecoregions are fairly arbitrary. It should be noted, however, that two of the three South African localities visited where *C. irenae* was not found are “Drakensberg montane grasslands, woodlands and forests” (Fig. 3), whose forest microhabitat structure is quite different from Maputaland. These habitats are further inland and at higher altitudes than *C. irenae* typically inhabits, perhaps indicating particular microclimatic, altitudinal and

habitat preferences. We predict that in the south the species inhabits Maputaland coastal forests into Mozambique, but that further north in tropical southern Africa, it continues inland into the adjacent ecoregion (the Zambebian and Mopane woodlands) as far north as Malawi. Although no specimen records currently exist from Mozambique and Swaziland, we predict that the species occurs there. Our data support the endemism hypothesis by 1) showing the continuity of the Maputaland forest mosaic ecoregion into Mozambique, and by 2) showing the ecoregion Zambebian and Mopane woodlands' adjacency to Maputaland. Where found, the *C. irenae* adult abundances were greatest during the beginning of our study (11–13 April 2006) while towards the end (28–29 April 2006) no further adults were found.

Habitat preference.—No *C. irenae* webs were measured in open canopy stands (Fig. 4C), which is not to be interpreted to mean that the spiders never occur there. In Maputaland *C. irenae* inhabits most tree habitats, including lone trees in semi-open canopy areas, and even synanthropic vertical surfaces, but preferentially occupies partially open and closed canopy stands. However, three of the four habitats where spiders and their webs were investigated in detail are forests (Fig. 4B), which is consistent with our assumption that forests and not other types of tree stands are the species' prime habitat. Evidently, the species is not confined to sand forests, refuting our hypothesis 2. We also conclude that *C. irenae* does not exclusively inhabit closed canopy forests (Fig. 4C), and is much more common in partially open stands (see below).

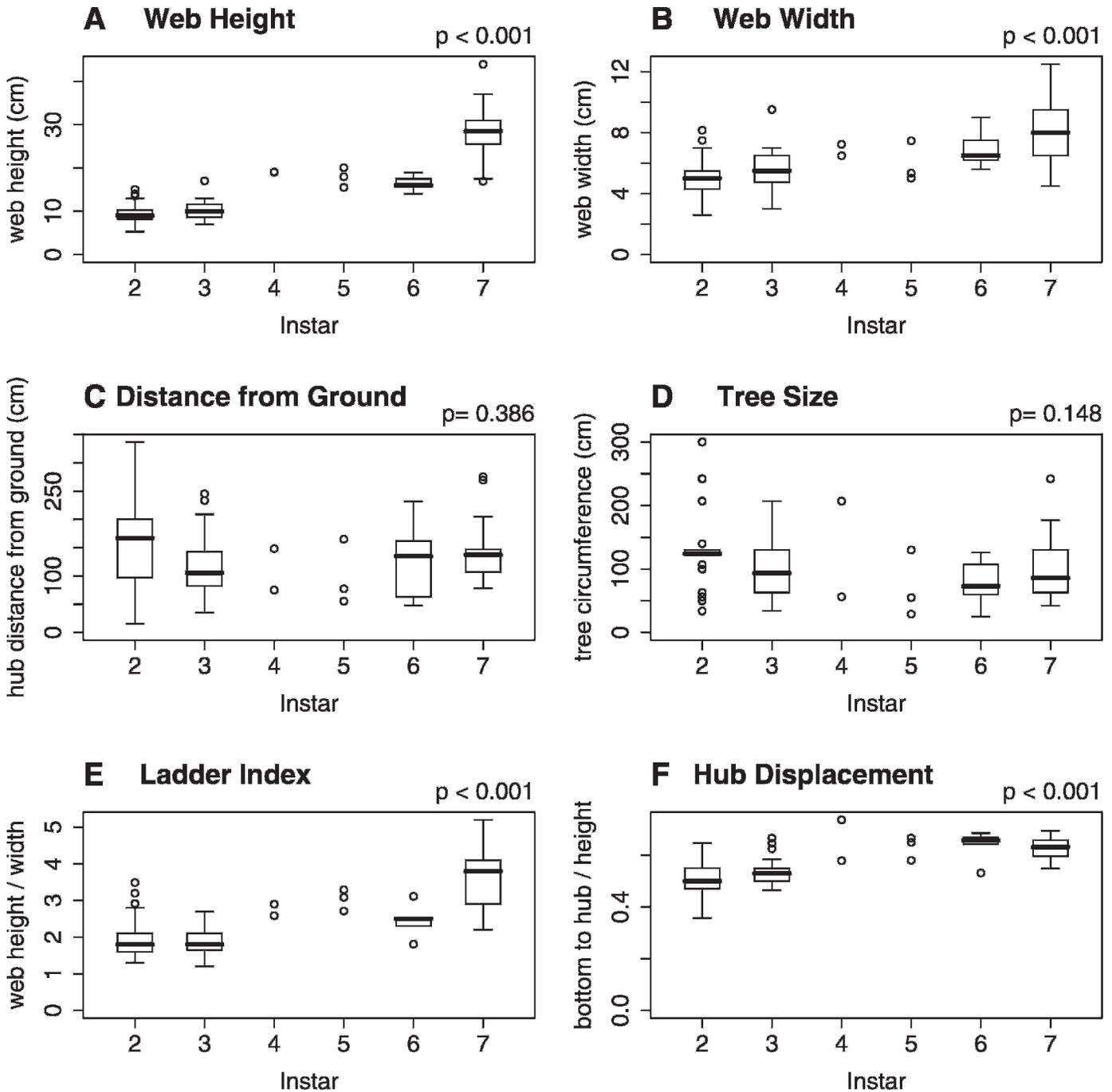


Figure 5.—*Clitaetra irenae* web parameters by spider size (instar number): A. Web height; B. Web width; C. Distance from ground; D. Tree size preference; E. Ladder index; F. Hub displacement. Differences between stages 2 and 7 were tested (Mann-Whitney U test), shown as P values.

Many trees with *C. irenae* webs ($n = 71$) could not be identified to species, but evidently *C. irenae* do not associate with one or a few particular tree taxa, nor with trees of a particular bark structure, refuting the hypotheses 3 and 5. This is reflected in the diverse habitats in which the species was encountered, each of which contains unique plant assemblages.

Our predictions that larger spiders chose larger, matured trees, and lower portions of trees, ignored web allometry and were based on the assumption that spider web size increases

with age. While the measured webs indeed increased with age (Figs. 5A, B) the fact that a variety of tree trunk sizes were utilized by each instar (Fig. 5D) refutes our hypothesis 4. Similarly, spiders of a certain age showed no preference for website height above ground (Fig. 5C) refuting the hypothesis 7. This would indicate a fair degree of tolerance to microclimatic variation with web height above ground (varying between 15.5 cm and 337.0 cm), which are expected to differ substantially from ground to canopy height. Dispersal of second instars and subsequent web construction

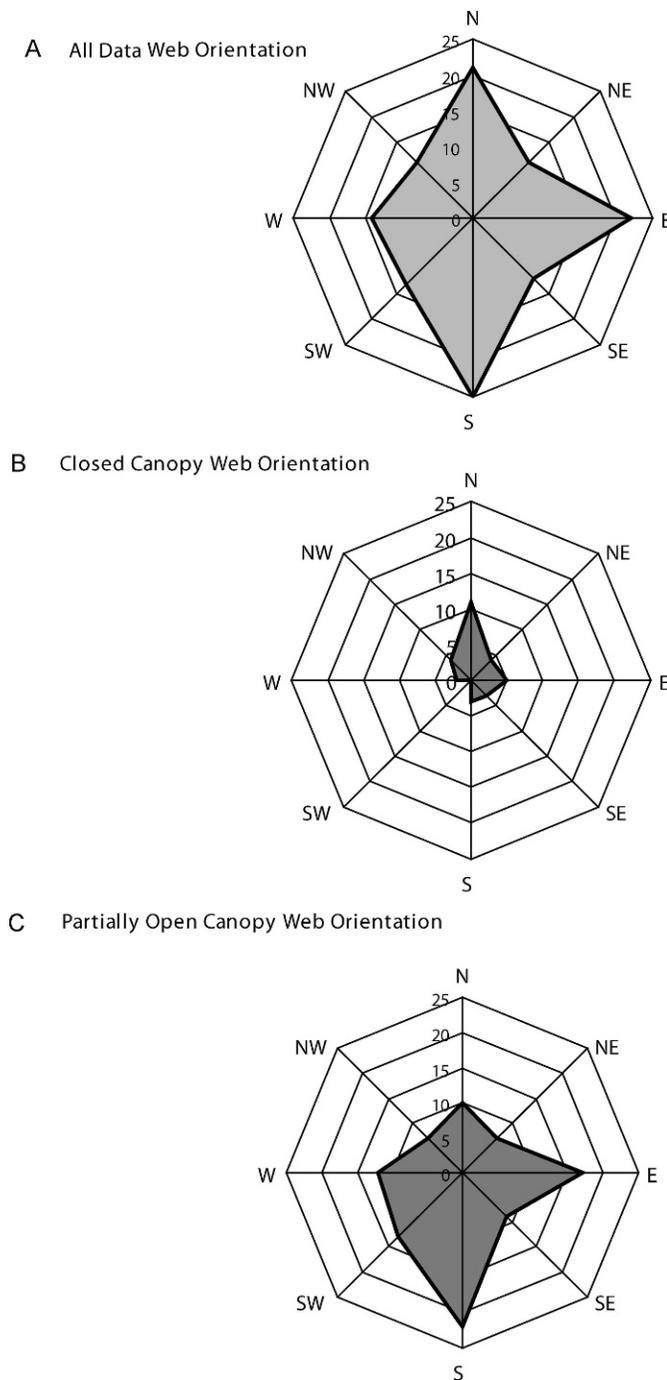


Figure 6.—*Clitaetra irenae* web orientation using circular statistics (Fisher 1993): A. All data (no orientation preference detected); B. Closed canopy forest (significantly north); C. Partially open canopy forest (significantly bimodal, south or east). Light versus dark grey graph colors represent statistically insignificant versus significant (Rayleigh test, $P < 0.05$) orientation.

appears to be in the immediate vicinity, and on the same tree, as the mother's web.

Web allometry.—The two indices quantifying the ontogenetic web changes from orb to ladder and the simultaneous hub displacement towards the top frame (Figs. 5E, F) both increase with spider size, which supports the prediction of

hypothesis 8. Such web allometry explains the lack of correlation between spider age and tree size. The ladder index, which is the relative web height, increases significantly with age, which is consistent with our initial observations of modified adult webs (Fig. 2). To a growing spider and its web the limiting factor on a tree of a given size is the horizontal website availability (tree circumference). The observed ontogenetic web allometry allows the growing spider's web to increase vertically, while at the same time the corresponding horizontal web increase is not required, allowing the spider to remain on the same tree. The smallest tree on which an adult female web was constructed (tree circumference 42.0 cm, web width 6.5 cm) would suggest that the curvature of the tree trunk may also play a role in the web site selection, making available points of attachment on the bottom and top of the web but eliminating the restriction of horizontal attachment points on the side of the web. We see the ladder web as an adaptation to an arboricolous life style because it eliminates the need of a potentially costly and dangerous walk from one (smaller) tree to another (larger) tree. Ants, which are abundant on trees where *C. irenae* occur, may be important predators (Kuntner 2006). However, ants are not known to invade webs. Thus, orb-web spiders may be safer from predators on (or close to) their webs than walking about.

The webs of all adult nephilid spiders have displaced hubs, mostly towards the top (for rare horizontal displacement in *Nephilengys*, see Kuntner 2007). Hubs are often displaced above the web center in other araneoid spiders with vertical webs (see Kuntner et al. 2008), notably in araneids. The logical explanation for an ontogenetic shift from a central hub in small juveniles towards the eccentricity seen in larger, heavier spiders is gravity. Masters & Moffat (1983) demonstrated that predation success of the araneid spider *Larinioides sclopetarius* (Clerck 1757) improves in webs with hubs displaced above the web center, as the time to reach the prey upwards and downwards is thus optimized.

Ladder webs on tree trunks, present in the extant species of the basal *Clitaetra-Herennia* grade, were the ancestral life style of the pan tropical clade Nephilidae and reversed to aerial orb webs in the ancestor of *Nephila* (Kuntner et al. 2008). All nephilids, *C. irenae* included, retain the non-sticky spiral (NSS) in their finished web unlike most other orbweavers (Kuntner 2006; Kuntner et al. 2008). NSS or auxiliary spiral functions as a guide during the spider's sticky spiral construction (Zschokke 1993). Unlike in *Nephila* and *Nephilengys*, NSS in *Clitaetra* webs is difficult to discern, perhaps because these spirals are thin and may get stuck with the narrowly meshed sticky ones. Kuntner (2006) determined the NSS presence by observing the spiders build at night (and not cutting the NSS when laying the sticky spiral), and the same could not be determined by photographs of finished webs. The retention of the NSS in nephilids has been suggested to have evolved in response to female gigantism (Hormiga et al. 1995). However, NSS seems to have been present in the nephilid ancestor, where sexual dimorphism was only moderate and not extreme (Kuntner et al. 2008). Perhaps the retention of NSS was originally related to ladder web architecture, and its presence in derived nephilids represents evolutionary time lag. The convergent presence of NSS in *Scoloderus* webs (below) may also be related to ladder web architecture.

While ladder web architecture is homologous in *Clitaetra* and *Herennia* (Kuntner et al. 2008), it is clearly not related to, and differs functionally from, other known araneoid ladder webs. For example, neotropical *Scoloderus* builds an extreme ladder and, as in nephilids, retains the NSS (Eberhard 1975: fig. 2), but this web is aerial, not arboricolous, and its hub is displaced to the lower, not upper frame of the web, making the spirals above the hub resemble a ladder. The hub of the extreme ladder web of an unidentified araneoid from New Guinea described by Robinson & Robinson (1972), however, is displaced up as in nephilids, but that web is aerial and apparently lacks the NSS. Furthermore, while nephilid ladder webs are permanent structures (Kuntner 2005, 2006; Kuntner et al. 2008), the above webs are taken down daily and rebuilt every night (Robinson & Robinson 1972; Eberhard 1975). Ladder webs apparently evolved convergently in araneids and nephilids, perhaps in order to exploit new websites (trees) or food resources. The first may be particularly true for nephilids: while no study has focused on the prey of *Clitaetra* and *Herennia* these spiders exploit tree trunks as websites and *Herennia* even evolved a unique web design using *pseudoradii* (Kuntner 2005; Kuntner et al. 2008). Eberhard (1975) pointed out that a ladder web architecture allows for a more constant mesh size than any circular orbweb, which may be related to specialization for certain prey types. Aerial ladder webs have been suggested to represent convergent adaptation for ensnaring moths (Eberhard 1975; Stowe 1978). However, prey capture in tropical spiders is often anecdotal. While Stowe (1978) showed that 68% of 212 prey items of *Scoloderus* were moths, Robinson & Robinson (1972) observed a single prey item, a moth, attracted into the ladder web of their unknown spider by a light source. Although the focus of our study was not a quantification of *C. irenae* prey, the few sporadically observed insect prey items in their webs (Fig. 1A–D: Orthoptera, Diptera, Lepidoptera (Pyrilidae), Homoptera) suggest that the species is an opportunistic predator not particularly specialized on moths.

Web orientation.—Superficially, *C. irenae* webs appear randomly oriented (Fig. 6A). However, preferential spider web orientation occurs in both closed and partially open canopy forests. In closed canopy forests (Fig. 6B) the spiders show a preference for the northern side of the tree, refuting the first part of the web orientation hypothesis (that no orientation preference would be shown in closed canopy forests). Two types of bark that were found under closed canopy (smooth, medium) both show a significant orientation to the north, which indicates that northern orientation of webs under closed canopy is related to canopy closure, not bark type. Conversely, in partially open canopy forests (Fig. 6C) the spiders preferentially chose southern and eastern faces of trees, which is supportive of the second part of our hypothesis 6.

Web orientation probably affects web microclimate. Prolonged direct sun exposure could harm the spider or its web, or may affect prey availability and/or predation pressure. In the southern hemisphere, the predicted preference for the southern, shady side of trees makes sense in a partially open forest. It is somewhat surprising, however, that the spiders inhabiting closed canopy forests seem to prefer a northern (perhaps warmer) orientation, where we predicted randomness, though

this result does not, per se, refute hypothesis 6. Since we mainly scored smooth barked trees in sand forests (all closed canopy) it is not surprising that the web orientation patterns on smooth bark trees resemble those of closed canopy forests (Fig. 6B). The preference for the southern and eastern sides of trees in partially open canopy habitats (Fig. 6C) would suggest an aversion for direct sunlight and a preference for darker sides of trees.

Implications for Maputaland ecology.—Previous Maputaland studies have focused on organisms such as dung beetles and birds to assess community heterogeneity and the impacts of habitat destruction and regeneration on faunal and floral components (Van Rensburg et al. 1999, 2000; Davis et al. 2002; Wassenaar et al. 2005). However, Maputaland arachnids are highly diverse, with 457 species recorded from the Ndumo Game Reserve, 10,112-ha in size (Haddad et al. 2006). Given such diversity it is likely that several species are endemic to Maputaland and could be used as indicators of changes and disturbances to habitats, including sand forest.

Spiders are generally more sensitive than other arthropod groups to the vegetative structural conditions in a habitat, particularly web-builders (e.g., Marc et al. 1999; Stiles & Coyle 2001; Finch 2005). In monitoring or habitat evaluation using spiders as bio-indicators, the absence of species typical for a habitat (stenotypic species) is often indicative of low habitat quality, including vegetation structure (Bonte & Maelfait 2001). Thus, the identification of a sensitive species in the Maputaland fauna could provide an indication of the current condition of forest patches and the extent of disturbance to which the local fauna is presently being exposed. Once identified, indicator spider species can also be used for long-term monitoring of landscapes (Bonte et al. 2002), which will enable conservationists to assess changes in the condition of these forests over time. A particularly important current conservation issue in South Africa is the impact of heavy utilization of sand forests by elephants in the Tembe Elephant Park, Maputaland. This is thought to lead to the irreversible opening up of the sand forest into a structure comparable to mixed woodland (W.S. Matthews pers. comm.), which is likely to have a strongly negative long-term effect on the plant and animal communities, and on the diversity of the sand forest. Additionally, the growing rural human population in Maputaland is putting increasing pressure on sand forest patches outside conservancies (Kirkwood & Midgley 1999).

In Africa, particularly, forests are opened up by big game, and such forest gaps are not necessarily indicative of unnatural disturbance. Indeed, in the reserve where elephants occur (Tembe), partially open canopy patches seem to be continuous with closed canopy sand forests. Thus, our finding of most individuals of *C. irenae* in partially open canopy forest stands does not refute our hypothesis about *C. irenae* dependence on the undisturbed Maputaland forest habitats. This could be an artifact of our under-sampling of closed canopy locations. Assuming that indigenous, undisturbed Maputaland forests are closed canopy, and thus the original preference of *C. irenae* spiders in a quality habitat is towards the north, scoring web orientation might be indicative of forest quality/disturbance. The easy *C. irenae* identification (Fig. 1, see Kuntner 2006) warrants further investigation as to whether it might be a suitable bioindicator.

Conclusions.—The data at hand suggest the ecological and behavioral dependence of *C. irenae* on the threatened Maputaland forests. The wider Maputaland endemism hypothesis receives support, but the hypotheses that *C. irenae* inhabits exclusively sand forests, mature trees, trees of a particular species, trees with a smooth bark, tree habitats at certain height above ground, and only closed canopy forest stands, are refuted. Evidently the species' ecological niche is flexible to an extent but requires suitable tree habitat under at least partially closed canopy. However, the web orientation on trees appears to be indicative of closed versus partially open canopy forest.

Conservationists may benefit from utilizing the available arthropod data in assessing the quality of tropical forests. The ecology of obligate arboricolous orb-weaving spiders (like the nephilids *Clitaetra* and *Herennia*), seems especially well suited for systematic conservation assessments in the (sub)tropics because they range from western Africa (Kuntner 2006) through South and Southeast Asia into Australasia (Kuntner 2005) where some species are narrow endemics and others appear to be widespread and invasive (Kuntner 2005, 2006). The "Africa + Asia + Australasia" tropical belt matches the maps of global biodiversity conservation priorities (Brooks et al. 2006), but also lies precisely in a zone of high population pressure and low human development index (see Jha & Bawa 2006), a detrimental combination of factors associated with heavy deforestation.

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