2018. Journal of Arachnology 46:13–20

Vertical distribution of wandering spiders in Central America

Witold Lapinski[1] and **Marco Tschapka**[1,2]: [1] Institute of Evolutionary Ecology and Conservation Genomics, University of Ulm, Albert-Einstein-Allee 11, 89069 Ulm, Germany; E-mail: wito.l@gmx.de; [2] Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa Ancón, República de Panamá

Abstract. We examined patterns of vertical distribution within an assemblage of seven species of large wandering spiders in a lowland rainforest on the Caribbean slope of Costa Rica. Over 16 months, 22 trees were surveyed regularly at night, up to a height of 43 m, using a rope climbing technique. Local climate and canopy microclimate exhibited only weak seasonal fluctuations. There was a distinct vertical segregation between ground-dwelling and arboreal species. The arboreal species used almost the entire available height range, whereby immature *Cupiennius coccineus* F.O.P.-Cambridge, 1901 occupied higher parts of the trees than adults. The two most abundant arboreal species differed also in their use of arboreal microhabitats: while *Cu. coccineus* occurred most frequently on trunk bark and on epiphyte leaves, the smaller *Ctenus* sp. 4 was more restricted to trunk bark. We detected effects of structural complexity of the host trees but no effects of canopy microclimate or of local climate on vertical distribution of *Cu. coccineus*, by far the most abundant arboreal species. The differences in vertical distribution both between age classes of *Cu. coccineus*, and between *Cu. coccineus* and the smaller *Ctenus* sp. 4 suggest size-dependent habitat segregation in arboreal species along the vertical axis, which might diminish cannibalism and/or intra-guild predation. Moreover, the wide range of vertical distribution of arboreal spiders suggests that they may connect the understory and canopy food webs.

Keywords: Canopy, Costa Rica, Ctenidae, epiphyte, tree

Rainforest canopies are fascinating but still poorly studied habitats. Since the pioneering days of canopy biology, the access techniques have been improved and now allow more thorough and sophisticated analyses of the processes in the tree tops (Mitchell et al. 2002; Lowman et al. 2013). In tropical forest canopies the bulk of arthropods is formed by insects and spiders (Basset 2001). Comprising 4.6–10.2% of all arthropod individuals, spiders exhibit high relative abundance in tropical forest canopies (Russel-Smith & Stork 1994; Floren & Deeleman-Reinhold 2005; Gurgel-Gonçalves et al. 2006; Marques et al. 2006). Mass-collecting by fogging is the most common technique to assess abundance and species diversity of canopy arthropods (Basset 2001). However, due to its destructive character, this technique is not suitable to examine ecological traits of target species that need repeated surveying in the canopy. Here, an inexpensive rope climbing technique (see Jepson 2000; Barker & Standridge 2002) provides more flexible survey possibilities as it allows observations on any tree at any height except for the outermost crown regions of climbed trees.

The ecology of most tropical spiders is still understudied. Large, wandering araneomorph spiders are often common in the tropics and may form assemblages of seven or more species (Höfer et al. 1994; Gasnier et al. 2002; Lapinski & Tschapka 2013). Observations on habitat use outside the canopy within a guild of araneomorph wandering spiders in a Costa Rican lowland rainforest revealed the existence of three distinct subguilds (Lapinski & Tschapka 2013). The **semi-aquatic species** *Ancylometes bogotensis* (Keyserling, 1877) (Ctenidae) and *Trechalea tirimbina* Silva & Lapinski, 2012 (Trechaleidae) were strongly associated with bodies of water. The **forest-ground dwellers** *Ctenus curvipes* (Keyserling, 1881)*, Ctenus sinuatipes* F.O.P.-Cambridge, 1897*,* and *Ctenus* sp. 3 (Ctenidae) roamed the forest floor and climbed only occasionally into the lower vegetation. The **vegetation dwellers** *Cupiennius coccineus* F.O.P.-Cambridge, 1901*, Cupiennius getazi* Simon, 1891*,* and *Phoneutria boliviensis* (F.O.P.-Cambridge, 1897) (Ctenidae) were found almost exclusively on plants. In the latter subguild, *Cu. coccineus* was most abundant in the forest and was also found to climb on trees, while the latter two species were found mainly on tall vegetation in treeless areas. Distinct differences in desiccation resistance among the species were related to habitat microclimate. Vegetation-dwelling species experienced drier and more variable microclimate than ground-dwelling and semi-aquatic species. Accordingly, vegetation dwellers showed higher desiccation resistance than species from the other two subguilds (Lapinski & Tschapka 2014). Differences in the ability to adhere to smooth surfaces and the corresponding morphological traits also matched the ecological preferences of these species (Lapinski & Tschapka 2013; Lapinski et al. 2015). All this provides evidence that species traits play a key role in shaping community structure (Kneitel & Chase 2004).

So far, ecology of large wandering spiders was mostly observed on and close to the forest floor (Höfer et al. 1994; Gasnier et al. 2002; Torres-Sánchez & Gasnier 2010). Thus, almost nothing is known about the vertical distribution of these spiders, its seasonal fluctuations or its underlying causes. To fill this gap, we surveyed 22 trees from ground to the canopy in a lowland rainforest at the Reserva Biológica Tirimbina on the Caribbean slope of Costa Rica.

We hypothesized that the known vegetation-dwelling species occur even higher than estimated and that the canopy would harbour additional species. We expected that arboreal species would be segregated vertically and that vertical distribution would depend on local climate or microclimate. Moreover, more heterogeneous habitats provide more shelters and food for any type of animals, both prey and predators. Therefore, arboreal wandering spider species should occur at greater heights and in greater densities on structurally complex host trees with many epiphytes than on less complex trees with few epiphytes.

METHODS

Study area.—Fieldwork was carried out from September 2010 to February 2012 at the Reserva Biológica Tirimbina (RBT; 10°24′ N, 84°07′ W, 180 – 220 m asl), Heredia Province, Costa Rica. Mean annual temperature is 25.3°C and mean annual precipitation is 3,777 mm. RBT includes very humid tropical pre-montane forest and transitions to very humid tropical forest. Eighty-five percent of the reserve's forest is classified as primary forest. RBT also encompasses areas of secondary forest of various age classes. The trees surveyed on an island in the Sarapiquí river were in old growth secondary forest, while the rest of the surveyed trees were in primary forest (see Fig. S1, online at http://dx.doi.org/10.1636/JoA-S-16-033.S1). Forest canopy height in the area ranged between 30 and 40 m, with emergent trees up to *ca.* 50 m. For a more detailed description, see Lapinski & Tschapka (2013).

Fieldwork.—Most fieldwork was conducted in the western part of RBT. We surveyed 22 trees belonging to 12 different species once per month (except December 2010 and March 2011), using rope climbing technique (Jepson 2000; Barker & Standridge 2002). A table of tree species and their characteristics is available online at http://dx.doi.org/10.1636/JoA-S-16-033.S3. As spiders are not usually host-tree specific, we surveyed suitable trees from different species (Sørensen 2003 and references therein). Selection criteria of suitable trees were (1) accessibility by an arrow shot from the ground in order to install a climbing rope and (2) height at least that of the surrounding canopy. Spiders were surveyed at night on trunks and central portions of the crown of each selected tree and its surrounding vegetation, from ground level to *ca.* 3 m above the branch to which the climbing rope was attached. Data were taken within a survey radius of approximately five meters and only during the ascension to prevent repeated sampling. Prior to ascension, we also searched for 15 minutes for spiders on the forest ground and in the understory vegetation within a 5-meter radius around the climbed tree, to collect data on spiders roaming the lower strata of the forest. Active spiders of different instars were recorded during 152 surveys, from 1830 – 0415 h. All spiders encountered at the entrance or outside of their day shelters were considered to be active. Only large araneomorph species with an adult body length $\geq$17 mm were included, to reduce a potential size-driven bias while searching for the spiders on the trees. These species were known from previous studies at RBT (Lapinski & Tschapka 2013, 2014; Lapinski et al. 2015) and thus could be identified in the field without the necessity of capturing and killing them. Even juveniles could be reliably identified in the field, as we had previous experience with captive individuals. We distinguished the following instar categories: subadult or adult, large juvenile (i.e., $\geq$0.5 the body length of adults), and small juvenile ($<$0.5 the body length of adults of the respective species). As the smallest juveniles (spiderlings $\leq$3 mm body length) could not be reliably located and identified in the field, they were omitted from our surveys. Spiders at greater distance from the climbing observer were identified using binoculars (Pentax 8x36 DCF HS). Spiders were never observed to flee when illuminated by head lamp or when a branch was shaken by the climber's movements. Voucher specimens of two previously unidentified species were preserved in ethanol (70%) and after successful identification will be deposited in the Museo de Zoología, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica.

For each individual spider sighting, the following parameters were recorded: date, time, tree individual, tree species, species of the spider, sex, instar, height above ground using a measuring tape (to the nearest 0.1 m), microhabitat (for categories, see Fig. 4). Tree species were identified using Condit et al. (2011) and with the help of the local botanist José Angel González Ramírez. To assess the influence of microclimate fluctuations on the vertical distribution of the spiders during the study period, data loggers (Hobo Pro v2, temperature/relative air humidity, Onset Computer Corporation, Cape Cod, MA, U.S.A.) were installed on three trees at 1 m and 28 m above ground on the northern side of the tree trunks (see supplementary material Table S3). Temperature (°C) and relative air humidity (%) were recorded hourly from 1 Oct 2010 to 27 Feb 2012 (for details see Lapinski & Tschapka 2014). Since the data loggers provide the exact time point of logging, temperature and relative air humidity-values were related to the full hour of encounter of each spider individual. Vapor pressure deficit is the force that drives evaporation (Anderson 1936; Gates 1980) and, therefore, we calculated vapor pressure deficit from the recorded temperature and relative air humidity data using the equation of Allen et al. (2005). Additionally, precipitation data obtained from the RBT meteorological unit were used to relate changes of local climate with vertical distribution patterns of the spiders.

Statistical tests.—In both inter- and intraspecific analyses, all instars were included unless otherwise indicated. We used SigmaStat (Version 3.5) for all univariate analyses and stepwise forward and multiple linear regressions. We tested for interspecific differences in the use of substrate type and microhabitat (nominal variables) with a Chi-square (χ^2) test. Continuous non-normally distributed variables were analyzed with Kruskal-Wallis one way ANOVA on ranks using Dunn's *post-hoc* test for unequal sample size. To make the vertical distribution of the spiders on trees of different height comparable, relative height of the spiders (rHS) on the respective tree was calculated (with values ranging between 0 and 1) and used instead of absolute height of the spiders above ground. Similarly, instead of absolute height of the lowest branch of a tree, its relative height (values between 0 and 1) was used for the analyses, the higher the value, the smaller the crown height relative to total tree height. To better visualize the vertical distribution of the two most common arboreal species, data on the relative height above ground of all observed individuals (all instars) were assembled in classes (0.0–0.2, 0.21–0.4, …0.81–1.0). We tested with a Chi-square for differences in the absolute numbers encountered in the classes.

Cupiennius coccineus was the by far most abundant arboreal species ($n = 880$) and we used the species' data as an example to explore the vertical distribution of large wandering spiders. To obtain densities of *Cu. coccineus* per surveyed tree, we divided abundance by total tree height, since due to varying structural complexity of the trees, no area values could be calculated. In order to explore which variables may affect density and vertical distribution of *Cu. coccineus* data were $\log_{10}(x+1)$ – transformed and then standardized. We used only the standardized data that we entered into stepwise forward

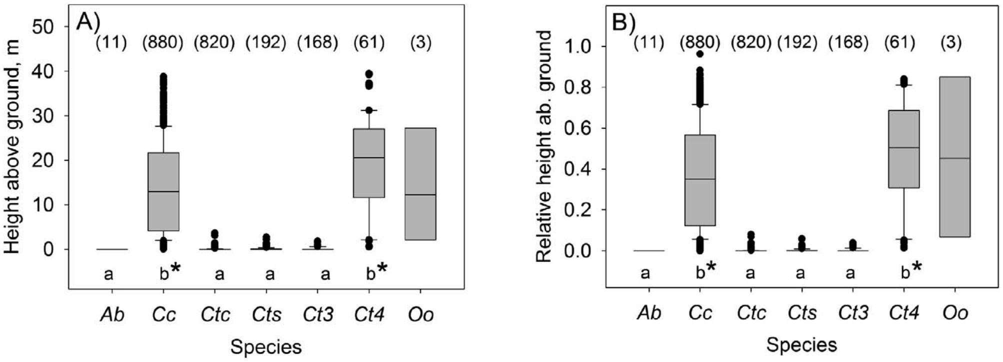

Figure 1.—Vertical distribution of wandering spiders at RBT expressed by (A) absolute height of the spiders above ground and (B) height of the spiders relative to the total height of the trees. Different letters below the boxes indicate significant differences in the *post hoc* test of Kruskal-Wallis ANOVA, asterisks point to significant difference in Mann-Whitney test, figures in parentheses above the boxes give the sample size. Horizontal lines in the boxes represent the median, boxes are from Q_{25} to Q_{75}, error bars from Q_{10} to Q_{90}, full circles are outliers. Species abbreviations: *Ab* = *Ancylometes bogotensis*, *Cc* = *Cupiennius coccineus*, *Ctc* = *Ctenus curvipes*, *Cts* = *Ctenus sinuatipes*, *Ct3*, *Ct4* = *Ctenus* sp. 3 and 4, respectively, *Oo*=*Olios obtusus*.

and then multiple linear regressions. We used only the data obtained on the climbed trees because structural characteristics of neighbouring vegetation were not assessed. Two approaches were applied. (1) To examine which structural variables may affect mean density of *Cu. coccineus* per survey on each tree we conducted stepwise forward linear regression. The number of tree individuals was the sample size ($n = 20$). Following independent variables were entered: diameter of tree trunk at breast height (DBH), tree height, relative height of the lowest branch, total number of holes (both on trunk and in the crown), and total number of epiphytes (both on trunk and in the crown) (see supplementary Table S4, available online at http://dx.doi.org/10.1636/JoA-S-16-033.S4). Subsequently, based on the results from that stepwise regression, we entered only those independent variables that may significantly contribute to the prediction of density of *Cu. coccineus*: DBH, relative height of the lowest branch, and total number of holes. The remaining independent variables did not add significantly to the prediction of density and were omitted from the multiple linear regression.

(2) To investigate how vertical distribution (i.e., relative height of spider above ground) may be affected we applied stepwise forward regression and subsequently multiple linear regression as described above. The difference was that each individual *Cu. coccineus* was treated as case and each tree was considered a replicate. Hence, in addition to the structural variables of the trees (DBH, height of tree, relative height of the lowest branch, number of epiphytes on the trunk, number of epiphytes in the crown, number of holes in the trunk, and number of holes within the crown), we were able to include instar, and vapor pressure deficit at 28 m above ground during the hour of spider encounter. Sample size was reduced from $n = 880$ to $n = 551$ individual observations made during the period from which microclimate data were available. First, we ran a stepwise forward regression on all variables and based on the results from that we entered only the following independent variables into a multiple linear regression: instar, DBH, height of tree, relative height of lowest branch, and number of epiphytes in the crown.

RESULTS

Twenty-two trees belonging to 12 species with a total height ranging from 26 to 47 m were regularly surveyed. Two trees (sp. 1, sp. 2) could not be identified because leaves and flowers could not be reached. We had to exclude two trees early during the study due to tree fall of neighboring trees that altered the site characteristics. Data already collected at these trees prior to the tree fall were included for assessing overall vertical distribution of the spider species (Figs. 1–3), the use of microhabitats and substrate types by the arboreal species (Fig. 4), and the seasonal fluctuations of vertical distribution of *Cu. coccineus* (Fig. 5).

Vertical distribution of the assemblage.—Data from 2136 individual observations from seven wandering spider species were recorded. Not a single individual of *Cu. getazi* and *P. boliviensis* was found within the forest. We found *Ancylometes bogotensis* only rarely because these spiders live mainly on banks of creeks and only three trees were close enough to water. *Ctenus curvipes*, *Ct. sinuatipes*, and *Ctenus* sp. 3 (Ctenidae) occurred mainly on or very close to the ground, rarely higher than 1 m (Fig. 1). *Cupiennius coccineus* and two previously undescribed species, *Ctenus* sp. 4 (Ctenidae) and *Olios obtusus* F.O. Pickard-Cambridge, 1900 (Sparassidae), were found almost exclusively on vegetation using almost the entire height range. *Cupiennius coccineus* and *Ctenus* sp. 4 occurred significantly higher than *A. bogotensis*, *Ct. curvipes*, *Ct. sinuatipes*, and *Ctenus* sp. 3 (Figs. 1 A, B, Kruskal-Wallis ANOVA, $P \leq 0.001$, for height of spider: $H_5 = 1755.2$, for relative height of spider: $H_5 = 1756.3$, Dunn's *post-hoc* test, $P < 0.05$). During all nocturnal tree surveys, only three individuals of *O. obtusus* were found, but during the walks to the surveyed trees several additional individuals were observed on understory vegetation, supporting the assignment of this species to the vegetation-dwelling subguild.

Vertical segregation of arboreal species.—The vertical distribution of *Cu. coccineus* and *Ctenus* sp. 4 overlapped strongly at intermediate heights (Fig. 2, all instars considered). However, *Cu. coccineus*, was more strongly represented in the lowest class of relative height, while *Ctenus* sp. 4 was more frequently found in the higher parts of the trees (Chi-squared

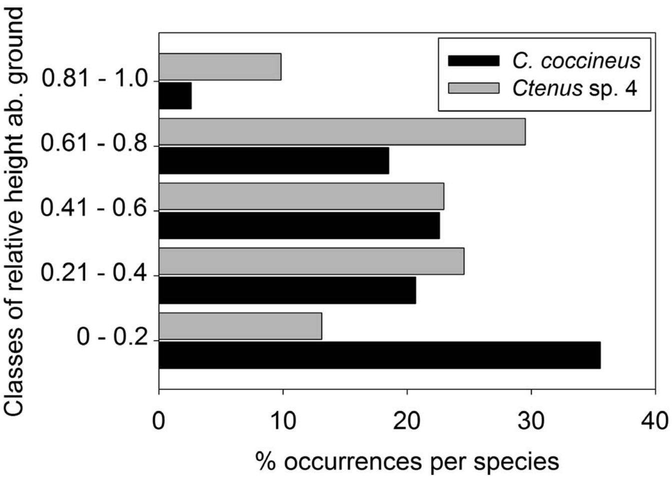

Figure 2.—Percentage of occurrences in different classes of relative height of spider above ground showing the vertical distribution of the arboreal *Cupiennius coccineus* ($n = 880$) and *Ctenus* sp. 4 ($n = 61$).

test, χ^2 = 22.08, df = 4, $P \leq 0.001$). Subadult/adult *Cu. coccineus* occurred significantly lower than both large and small juveniles, although the vertical distribution of all instars strongly overlapped (Fig. 3A, Kruskal-Wallis ANOVA, $P \leq 0.001$, $H_2 = 32.3$, Dunn's *post-hoc* test, $P < 0.05$). In *Ctenus* sp. 4, we found no such differences among the instars (Fig. 3B, Kruskal-Wallis ANOVA, $P = 0.628$, $H_2 = 0.93$).

Arboreal microhabitats.—*Cupiennius coccineus* and *Ctenus* sp. 4 differed significantly in microhabitat and substrate preferences (Fig. 4 A,B). Tree trunks and epiphytes on tree trunks were preferred by *Cu. coccineus* while *Ctenus* sp. 4 showed a more pronounced preference for tree trunks (Chi-squared test, $\chi^2 = 140.2$, df = 10, $P \leq 0.001$). Accordingly, *Cu. coccineus* preferred bark and leaf substrates, and *Ctenus* sp. 4 was mostly found on bark and moss (Chi-squared test, χ^2 = 133.6, df = 7, $P \leq 0.001$)

Seasonality.—Local climate at RBT showed no pronounced seasonality between September 2010 and February 2012. The two phases of reduced precipitation and higher vapour pressure deficit in April 2011 and February 2012 did not coincide with a clear change in vertical distribution of *Cu. coccineus* (Fig. 5). However, the position on the trees was significantly lower in September 2010 than in April 2011 (Kruskal-Wallis ANOVA, $P = 0.041$, $H_{15} = 25.7$, Dunn's *post-hoc* test, $P < 0.05$). In *Ct. curvipes*, *Ct. sinuatipes*, and *Ctenus* sp. 3, relative height of spiders was consistently below 0.1 and vertical distribution did not differ significantly among months (Kruskal-Wallis-ANOVA, $P = 0.704$, $H_{15} = 11.7$; $P = 0.162$, $H_{15} = 20.3$; and $P = 0.304$, $H_{15} = 17.2$, respectively). Sample size of *Ctenus* sp. 4 was too low to analyze seasonality in vertical distribution of that species.

The arboreal *Cupiennius coccineus*.—Because *Cu. coccineus* was by far the most abundant species on trees, we examined the variables affecting its density and vertical distribution in more detail. Density of *Cu. coccineus* varied significantly among individual trees and showed considerable variation among surveys (Kruskal-Wallis ANOVA on ranks H_{19} = 133.03, $P \leq 0.001$; see Fig. S2, available online at http://dx.doi.org/10.1636/JoA-S-16-033.S2).

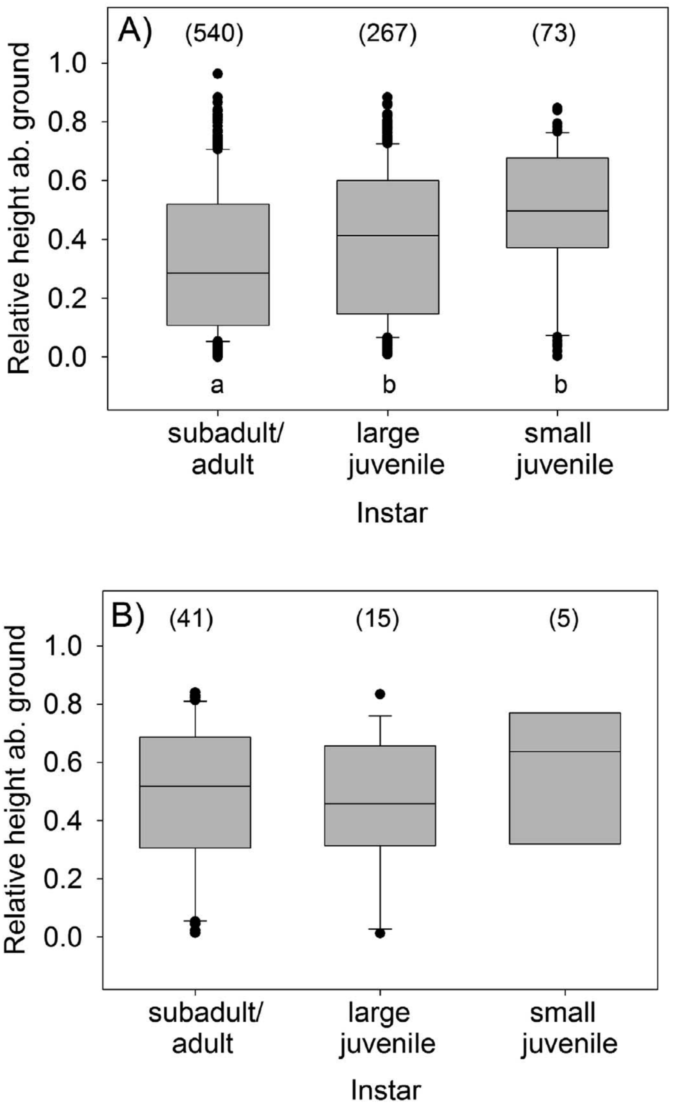

Figure 3.—Vertical distribution of different instars of (A) *Cupiennius coccineus* and (B) *Ctenus* sp.4. Instar abbreviations: sa/a=subadult/adult females and males, j2=large juveniles, j1=small juveniles. Different letters below the boxes indicate significant differences, figures in parentheses above the boxes show sample size. Horizontal lines in the boxes represent the median, boxes are from Q_{25} to Q_{75}, error bars from Q_{10} to Q_{90}, full circles are outliers.

Density of *Cu. coccineus* increased with the diameter at breast height, the relative height of the lowest branch and the number of holes (multiple linear regression, Table 1). The relative height of *Cu. coccineus* on trees was lower for late than for young instars, and decreased with tree diameter and the height of the lowest branch. It increased with height of the tree and with the number of epiphytes in the canopy (multiple linear regression, Table 2). The effect of instar and epiphytes is congruent with intraspecific differences in vertical distribution (Fig. 3) and microhabitat and substrate use (Fig. 4).

DISCUSSION

We explored the distribution of seven large araneomorph wandering spiders in a Costa Rican rainforest along vertical

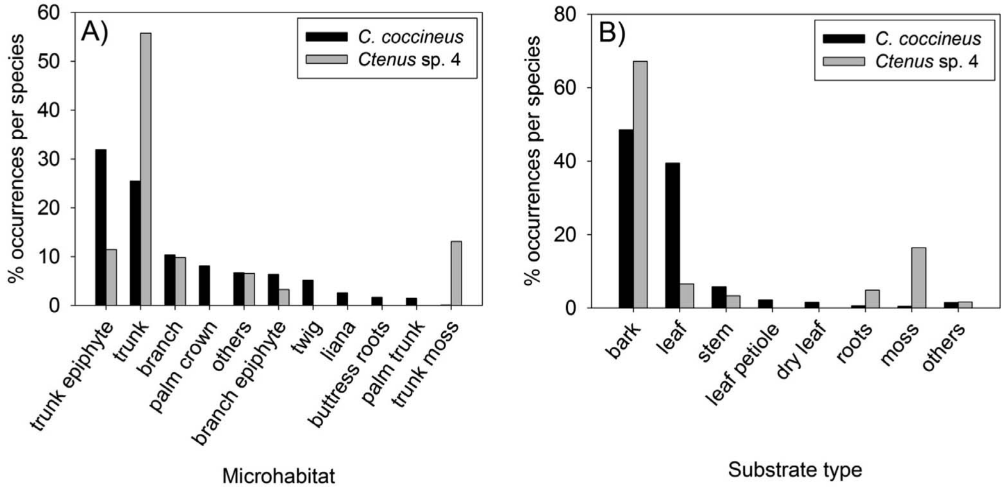

Figure 4.—Use of (A) microhabitats and (B) substrate types by the arboreal species *Cupiennius coccineus* ($n = 880$) and *Ctenus* sp. 4 ($n = 61$).

transects (i.e., trees). Lapinski & Tschapka (2013) suggested that the large wandering spiders at the study site may differ significantly in their vertical distribution, with *Cu. coccineus* being the most common arboreal species. However, these data were obtained mainly from the ground and surveys were limited mostly to a maximum height of 5 m. The current study overcomes these limitations and presents a more complete picture of a guild of large wandering spiders in a Neotropical rainforest. It confirms that *Ancylometes bogotensis*, *Ct. sinuatipes*, *Ct. curvipes* and *Ctenus* sp. 3 are indeed restricted to the forest ground and lower understory. The vegetation-dwelling subguild of large araneomorph wandering spiders, consisting of *Cu. coccineus*, *Cu. getazi*, and *P. boliviensis* (Lapinski & Tschapka 2013) is extended by two rare medium-sized species: *Ctenus* sp. 4 (Ctenidae) and *O. obtusus* (Sparassidae), which, together with *Cu. coccineus*, are rather arboreal and use nearly the entire height range. The data confirm our hypotheses that the known vegetation-dwelling species occur even higher than had been estimated and that the canopy would harbour additional species. However, more

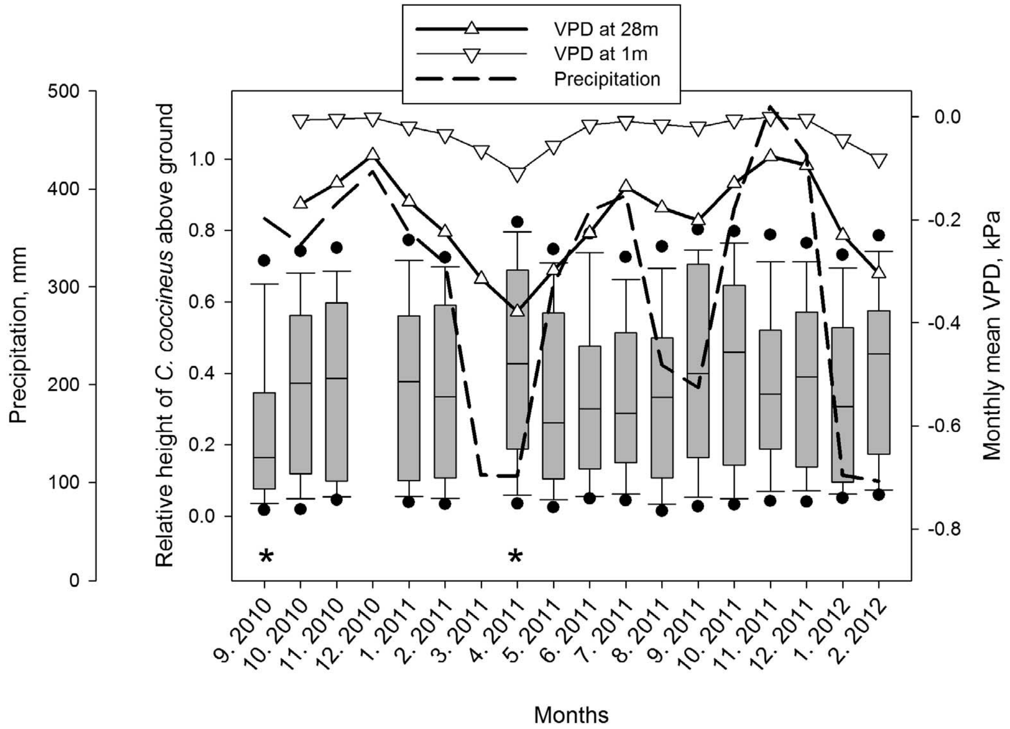

Figure 5.—Seasonal fluctuations of vapor pressure deficit (VPD) 1m and 28 m above the ground, precipitation, and relative height above ground (rHS) of *Cupiennius coccineus* (box plots, all instars included). Asterisks indicate significantly lower positions of *Cu. coccineus* relative to the remaining months. Horizontal lines in the boxes represent the median, boxes are from Q_{25} to Q_{75}, error bars from Q_{10} to Q_{90}, full circles are outliers within 5%- and 95%-percentiles.

Table 1.—Results of multiple regression analysis with density of *Cupiennius coccineus* on $n = 20$ trees as dependent variable and DBH, relative height of lowest branch, and total number of holes as independent variables. For definitions and details of variables see Table S4, available online at http://dx.doi.org/10.1636/JoA-S-16-033.S4.

	Coefficient	Std. Error	t	P	VIF
Constant	-7.97E-16	0.13	-6.16E-15	1	
DBH	0.69	0.15	4.71	<0.001	1.22
rel. height lowest branch	0.58	0.15	3.82	0.002	1.31
total number of holes	0.44	0.15	2.89	0.011	1.31
Analysis of Variance:					
	DF	SS	MS	F	P
Regression	3	13.64	4.55	13.57	<0.001
Residual	16	5.36	0.33		
Total	19	19	1		
$R = 0.85$	$R^2 = 0.72$	Adj $R^2 = 0.67$			
SE of estimate = 0.58					

data on the ecology of the apparently rare *O. obtusus* are needed. In Puerto Rico, an *Olios* species was the most abundant large wandering spider on low understory vegetation (Formanowicz et al. 1981). The arboreal katydid *Philophyllia ingens* (Tettigoniidae) showed a similarly wide range of vertical distribution with conspicuous movements upwards at dawn and downwards starting at noon (Fornoff et al. 2012). Because we did not find any single individual of *Cu. getazi* and *P. boliviensis* within the forest at any height, our suggestion that these vegetation dwelling species are restricted to early succession habitats is corroborated (Lapinski & Tschapka 2013). However, the cause for the habitat segregation among *Cu. coccineus* on the one hand, and *Cu. getazi* and *P. boliviensis* on the other hand remains unclear.

In ecological networks of wooded savannah of central Kenya, mainly ground-dwelling rather than arboreal predators couple food webs of canopy and grass strata by feeding on ground-dwelling as well as on fallen arboreal animals (Pringle & Fox-Dobbs 2008). In structurally much more complex rainforest networks, however, arboreal generalist predators with a broad range of vertical distribution and microhabitats, such as the common *Cu. coccineus*, appear to be the more efficient link between the understory and the canopy of the forest. These spiders may feed on occasionally climbing ground-dwelling prey, on understory residents and on canopy specialists. Both in Ecuador and in Costa Rica, the rainforest canopy and understory have distinct assemblages of fruit-feeding butterflies of the family Nymphalidae (DeVries et al. 2011). Through their wide vertical range, the studied arboreal spiders might exploit both understory and canopy Lepidoptera, and probably also other insects that segregate similarly along the vertical axis. Additionally, the spiders might be preyed upon by both understory and canopy predators, thus being an integral part of a complex network.

Microclimate may affect habitat use via physiology (Kneitel & Chase 2004; Morin 2011) and vertical distribution of generalist predators may mainly depend on their tolerance to environmental conditions (Basset et al. 2003). Thus, the pattern of vertical distribution at Reserva Biológica Tirimbina (RBT) can be largely explained by the interaction between spider physiology and the microclimate gradient along the vertical axis. Like other forests (Parker & Brown 2000; Madigosky 2004), the forest at RBT shows a gradient of decreasing temperature, increasing relative air humidity, and decreasing variation of both from the forest canopy to the ground (Lapinski & Tschapka 2014). Accordingly, the semi-aquatic and ground-dwelling species at RBT had lower desiccation resistance than vegetation-dwelling species, with *Cu. coccineus* showing the lowest susceptibility to water loss (Lapinski & Tschapka 2014). Similar links between physiology

Table 2.—Results of multiple regression analysis with relative height of ($n = 551$) *Cupiennius coccineus* on $n = 20$ trees as dependent variable and instar, DBH, height of tree, relative height of lowest branch, and number of epiphytes in the crown as independent variables. For definitions and details of variables see Table S4, available online at http://dx.doi.org/10.1636/JoA-S-16-033.S4.

	Coefficient	Std. Error	t	P	VIF
Constant	8.70E-03	0.04	2.20E-01	0.825	
instar	-0.18	0.04	-4.67	<0.001	1
DBH	-0.35	0.06	-5.57	<0.001	2.52
height of tree	0.46	0.07	6.64	<0.001	3.16
rel. height lowest branch	-0.16	0.07	-2.55	0.011	2.71
epiphytes in crown	0.18	0.05	3.81	<0.001	1.31
Analysis of Variance:					
	DF	SS	MS	F	P
Regression	5	88.54	17.71	20.92	<0.001
Residual	545	461.39	0.85		
Total	550	549.93	1		
$R = 0.40$	$R^2 = 0.16$	Adj $R^2 = 0.15$			
SE of estimate = 0.92					

and habitat use were found in other animal taxa, such as ants (Hood & Tschinkel 1990), frogs (e.g., Buttemer 1990; Young et al. 2005), and lizards (Eynan & Dmi'el 1993). Furthermore, we expected vertical distribution of arboreal species to depend on fluctuations of local climate or microclimate, which was not confirmed. Vapor pressure deficit during spider encounters did not add significantly to predict relative height of *Cu. coccineus* and seasonal fluctuations of precipitation at RBT were too weak to cause significant seasonal differences in vertical distribution in that species. This may result from its high desiccation resistance (Lapinski & Tschapka 2014); thus, even higher on the trees the microclimate may still be suitable for the species throughout the entire study period at the study site. In contrast, the three ground-dwelling *Ctenus* species occurred on or near the forest ground during the entire study period, even during wetter periods. This suggests that, due to their low tolerance to desiccation, the microclimate already becomes unfavourable for these species at low heights. Similarly, there was no significant effect of weekly rainfall on the activity density of spiders on lower parts of tree trunks in central Amazonia (Gasnier et al. 1995).

Moreover, microhabitat choice and hence vertical distribution of the studied spiders was also linked to morphology, with relatively bigger tarsal claw tufts (bearing adhesive setae) in the vegetation-dwelling than in the ground-dwelling species. The semi-aquatic species even lack these adhesive structures completely (Lapinski et al. 2015). These morphological characteristics result in better adhesion capabilities on smooth surfaces such as leaves or insect cuticle in the vegetation-dwelling compared to ground-dwelling and semi-aquatic species (Lapinski & Tschapka 2013). Similar relations between morphology, microhabitat choice, and vertical distribution are well documented for example in *Anolis* lizards (Polychrotidae, Elstrott & Irschick 2004) and in arboreal carabid beetles (Ober 2003).

The data only partially confirm our hypothesis that arboreal species are segregated vertically. Despite considerable overlap, the subtle differences in vertical distribution and microhabitat preferences together with low densities may reduce cannibalism, intraguild predation and competition among the instars of *Cu. coccineus* and the smaller *Ctenus* sp. 4. In this context, intraspecific differences in habitat use of the different instars have been observed, for example, in the predatory aquatic bug *Notonecta hoffmani* (Notonectidae, reviewed by Morin 2011), the theraphosid *Ephebopus murinus* (Walckenaer, 1937) (Marshall & West, 2008), and the co-occurring ctenid wandering spiders *Phoneutria fera* Perty, 1833, and *Phoneutria reidyi* (F.O.P.-Cambridge, 1897) (Torres-Sánchez & Gasnier 2010).

The results corroborate our expectation that on structurally more complex host trees, arboreal wandering spider species should also occur in greater heights and in greater densities than on less complex trees. The amount of epiphytes in the crown may affect vertical distribution of *Cu. coccineus* and thus form key components of the microhabitats, representing refuge sites for both the spiders and for their potential prey. Total number of holes may influence density of that species on the host trees. High complexity of vegetation may enhance densities of arthropods through providing both predators and their prey with shelter and food (Halaj et al. 1998; Stunz et al. 2002; Teixeira de Souza & Martins 2004). Experiments revealed the importance of structural complexity of plants for vertical distribution of spiders (Scheidler 1990), and for abundance and diversity of both spiders and potential prey arthropods (Halaj et al. 2000). Structurally complex canopies may also maintain higher densities of arthropods. High availability of shelters may lower predation on arthropods by actively hunting predators such as ants and birds because they need longer to find prey than in microhabitats with low structural complexity and hence low availability of shelters (Šipoš & Kindlmann 2012). High occurrence of epiphytes may not only enhance the structural complexity of trees but also the food supply for insects through vegetative parts, inflorescences and the associated fauna (Teixeira da Souza & Martins 2004).

In conclusion, our results demonstrate clear segregation between tree- and ground-dwelling species of large araneomorph wandering spider species in the rainforest, with only weak vertical segregation between arboreal species, which were used almost the entire height range. Vertical distribution of species may be the result of species-specific interactions between morphology and physiology on the one hand and microclimate and structural parameters of the host trees on the other. Given the wide range of vertical distribution of the studied arboreal spiders, they may couple the ecological networks of rainforest understory and canopy. Well planned long-term experiments are needed to investigate in more detail the factors promoting the observed dominance of *Cu. coccineus*, the role structural parameters play in microhabitat choice and vertical distribution within rainforests, and the coupling potential of these generalist predators. Similar surveys at other tropical sites are necessary to allow generalizations about the causes of vertical distribution of generalist arthropod predators.

ACKNOWLEDGMENTS

The Ministerio de Ambiente, Energía y Telecomunicaciones (MINAET) kindly granted us the permission to conduct the field work in Costa Rica. The friendly assistance of Javier Guevara (MINAET) is greatly appreciated. We are very grateful to all staff members at the Reserva Biológica Tirimbina for all their friendliness, support and for allowing us to realize this project at the station. Many thanks to José Angel González Ramírez (Organization for Tropical Studies) for identification of some trees and to Simone Blomenkamp for creating the map of RBT and assistance during tree preparation. Thanks to the editor and two anonymous reviewers for their suggestions which helped very much to improve the manuscript.

LITERATURE CITED

Allen, R.G., I.A. Walter, R. Elliott, T. Howell, D. Itenfisu & M. Jensen. 2005. The ASCE standardized reference evapotranspiration equation. Pp. 11–15. *In* Task Committee on Standardization of Reference Evapotranspiration of the Environmental and Water Resources Institute of the American Society of Civil Engineers. Reston, Virginia, USA.

Anderson, D.B. 1936. Relative humidity or vapor pressure deficit. Ecology 17:277–282.

Barker, M. & N. Standridge. 2002. Ropes as a mechanism for canopy access. Pp. 13–23. *In* The Global Canopy Handbook. Techniques of Access and Study in the Forest Roof. (A.W. Mitchell, K. Secoy, T. Jackson (eds.)). Global Canopy Programme, Oxford, UK.

Basset, Y. 2001. Invertebrates in the canopy of tropical rain forests. How much do we really know? Plant Ecology 153:87–107.

Basset, Y., P.M. Hammond, H. Barrios, J.D. Holloway & S.E. Miller. 2003. Vertical stratification of arthropod assemblages. Pp. 17–27. *In* Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy. (Y. Basset, V. Novotny, S. E. Miller & R.L. Kitching (eds.)). Cambridge University Press, Cambridge, UK.

Buttemer, W.A. 1990. Effect of temperature on evaporative water loss of the Australian tree frogs *Litoria caerulea* and *Litoria chloris*. Physiological Zoology 63:1043–1057.

Condit, R., R. Pérez & N. Daguerre. 2011. Trees of Panama and Costa Rica. Princeton Field Guides. Princeton University Press, Princeton, New Jersey, USA.

DeVries, P. J., L.G. Alexander, I.A. Chacón & J.A. Fordyce. 2011. Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. Journal of Animal Ecology 81:472–482.

Elstrott, J. & D.J. Irschick. 2004. Evolutionary correlations among morphology, habitat use and clinging performance in Carribean *Anolis* lizards. Biological Journal of the Linnean Society 83:389–398.

Eynan, M. & R. Dmi'el. 1993. Skin resistance to water loss in agamid lizards. Oecologia 95:290–294.

Floren, A. & C. Deeleman-Reinhold. 2005. Diversity of arboreal spiders in primary and disturbed tropical forests. Journal of Arachnology 33:323–333.

Formanowicz, D.R. Jr., M.M. Stewart, K. Townsend, F.H. Pough & P.F. Brussard. 1981. Predation by giant crab spiders on the Puerto Rican frog *Eleutherodactylus coqui*. Herpetologica 37:125–129.

Fornoff, F., D.K.N. Dechmann & M. Wikelski. 2012. Observation of movement and activity via radio-telemetry reveals diurnal behavior of the Neotropical katydid *Philophyllia ingens* (Orthoptera: Tettigoniidae). Ecotropica 18:27–34.

Gasnier, T.R., A.C. Azevedo, M.P. Torres-Sánchez & H. Höfer. 2002. Adult size of eight hunting spider species in central Amazonia: Temporal variations and sexual dimorphisms. Journal of Arachnology 30:146–154.

Gasnier, T.R., H. Höfer & A.D. Brescovit. 1995. Factors affecting the "activity density" of spiders on tree trunks in an Amazonian rainforest. Ecotropica 1:69–77.

Gates, D. M. 1980. Biophysical Ecology. Springer-Verlag, New York, USA.

Gurgel-Gonçalves, R., A.R.T. Palma, P.C. Motta, M.E. Bar & C.A.C. Cuba. 2006. Arthropods associated with the crown of *Mauritia flexuosa* (Arecaceae) palm trees in three different environments from Brazilian cerrado. Neotropical Entomology 35:302–312.

Halaj, J., D.W. Ross & A.R. Moldenke. 1998. Habitat structure and prey availability as predictors of the abundance and community organization of spiders in western Oregon forest canopies. Journal of Arachnology 26:203–220.

Halaj, J., D.W. Ross & A.R. Moldenke. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos 90:139–152.

Höfer, H., A.D. Brescovit & T.R. Gasnier. 1994. The wandering spiders of the genus *Ctenus* (Ctenidae: Araneae) of Reserva Adolfo Ducke, a rainforest reserve in central Amazonia. Andrias 13:81–98.

Hood, W.G. & W.R. Tschinkel. 1990. Desiccation resistance in arboreal and terrestrial ants. Physiological Entomology 15:23–35.

Jepson, J. 2000. The Tree Climber's Companion. A Reference and Training Manual for Professional Tree Climbers. 2nd ed. Beaver Tree Publishing, Longville, U.S.A.

Kneitel, J.M. & J.M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecology Letters 7:69–80.

Lapinski, W. & M. Tschapka. 2013. Habitat use in an assemblage of Central American wandering spiders. Journal of Arachnology 41:151–159.

Lapinski, W. & M. Tschapka. 2014. Desiccation resistance reflects patterns of microhabitat choice in a Central-American assemblage of wandering spiders. Journal of Experimental Biology 217:2789–2795.

Lapinski, W., P. Walther & M. Tschapka. 2015. Morphology reflects microhabitat preferences in an assemblage of Neotropical wandering spiders. Zoomorphology, DOI 10.1007/s00435-015-0257-8

Lowman, M.D., T.D. Schowalter & J.F. Franklin. 2013. Methods in Forest Canopy Research. University of California Press, Berkeley, Los Angeles, U.S.A., London, UK.

Madigosky, S.R. 2004. Tropical microclimatic considerations. Pp. 24–48. *In* Forest Canopies. 2nded.,(M.D. Lowman, H.B. Rinker, eds.). Elsevier Academic Press, San Diego, U.S.A.

Marques, M.I., J. Adis, G.B. dos Santos & L.D. Battirola. 2006. Terrestrial arthropods from tree canopies in the Pantanal of Matto Grosso, Brazil. Revista Brasileira de Entomologia 50:257–267.

Marshall, S.D. & R. West. 2008. An ontogenetic shift in habitat use by the Neotropical tarantula *Ephebopus murinus* (Araneae, Theraphosidae, Aviculariinae). Bulletin of the British Arachnological Society 14:280–284.

Mitchell, A.W., K. Secoy & T. Jackson (eds.). 2002. The Global Canopy Handbook. Techniques of Access and Study in the Forest Roof. Global Canopy Programme, Oxford, UK.

Morin, P.J. 2011. Community Ecology. Wiley-Blackwell, Chichester, UK.

Ober, K. 2003. Arboreality and morphological evolution in ground beetles (Carabidae: Harpalinae): testing the taxon pulse model. Evolution 57:1343–1358.

Parker, G.G. & M J. Brown. 2000. Forest canopy stratification – is it useful? American Naturalist. 155:473–484.

Pringle, R.M. & K. Fox-Dobbs. 2008. Coupling of canopy and understory food webs by ground-dwelling predators. Ecology Letters 11:1328–1337.

Russell-Smith, A. & N.E. Stork. 1994. Abundance and diversity of spiders from the canopy of tropical rainforests with particular reference to Sulawesi, Indonesia. Journal of Tropical Ecology 10:545–558.

Scheidler, M. 1990. Influence of habitat structure and vegetation architecture on spiders. Zoologischer Anzeiger 225:333–340.

Šipoš, J. & P. Kindlmann. 2012. Effects of the canopy complexity of trees on the rate of predation of insects. Journal of Applied Entomology 137:445–451.

Sørensen, L.L. 2003. Stratification of the spider fauna in a Tanzanian forest. Pp. 92–101. *In* Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy. (Y. Basset, V. Novotny, S.E. Miller, R.L. Kitching, eds.). Cambridge University Press, Cambridge, UK.

Stunz, S., C. Ziegler, U. Simon & G. Zotz. 2002. Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama. Journal of Tropical Ecology 18:161–176.

Teixeira da Souza, A.L. & R.P. Martins. 2004. Distribution of plant dwelling spiders: inflorescences versus vegetative branches. Australian Ecology 29:342–349.

Torres-Sánchez, M.P. & T.R. Gasnier. 2010. Patterns of abundance, habitat use and body size structure of *Phoneutria reidyi* and *P. fera* (Araneae: Ctenidae) in a Central Amazonian rainforest. Journal of Arachnology 38:433–440.

Young, J.E., K.A. Christian, S. Donnellan, C.R. Tracy & D. Parry. 2005. Comparative analysis of cutaneous evaporative water loss in frogs demonstrates correlation with ecological habits. Physiological and Biochemical Zoology 78:847–856.

Manuscript received 31 May 2016, revised 21 July 2017.