Chapter 7
Tarantulas and Their Habitats

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Abstract New World Theraphosidae inhabit a great variety of habitats from deserts and semi-deserts, grasslands to forests of all types. Many species thrive in man-made habitats such as soccer fields and backyards, others prefer pristine regions. High Andean species occur even above 4000 m a.s.l., others dwell in Mexican and Brazilian caves. Based on their lifestyles, they may be assigned to two main sub-guilds: terrestrial and vegetation dwelling. Many terrestrial species make burrows in the soil (fossorial species), others hide under various objects on the ground like stones or logs without constructing burrows. The vegetation dwellers may use different plant types, mainly trees and their epiphytes up to more than 35 m above ground (arboreal species) or are restricted to certain plants like terrestrial tank bromeliads. Many arboreal species thrive also on buildings. In some species small juveniles use different microhabitats than later instars (ontogenetic habitat shift). Local assemblages may contain several species which either use slightly different areas or heights of the habitat, differ in their basic life style or use the same patch of habitat at different times. However, habitat use by Theraphosidae at various scales and their community ecology have been largely neglected by arachnologists being focused mainly on tarantula taxonomy and systematics. Knowledge of habitat use by tarantulas, both at local assemblage level and at regional level may contribute greatly to a better understanding of the biology of these fascinating and beautiful animals as well as to their conservation.

7.1 Introduction

Everything in the universe is interconnected. Imagine visiting a square kilometer of any habitat; let us say a semi-desert in Mexico or a tropical lowland rainforest along the Amazon. What tarantula assemblage will you find there, consisting of how many species? Which species? And now it becomes even more interesting, now it becomes beautiful. How do they share the habitat? Are there intraspecific differences in life

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style among instars? What traits are linked to their specific lifestyles? Why are some of the species strongly associated with undisturbed habitats while others may also thrive on football fields or buildings? To what extent are arboreal tarantulas really arboreal and am I afraid of heights preventing me from investigating this?

Scanning the existing literature for basic life history information of Theraphosid species results all too often in rather minimalistic statements, even in the recent millennium. Basically we are stuck in the naming and counting process. Why are we not three or four steps further than that? Most studies on tarantulas deal with their taxonomy and systematics but it seems the chaos is still unresolved. Some authors have included more or less detailed natural history paragraphs to descriptions of species or taxonomic revisions (e.g., Indicatti et al. 2008; West et al. 2008; Mendoza 2014a, b; Kaderka 2015; Fukushima and Bertani 2017; Ferretti et al. 2018), sometimes even mentioning other tarantula species living in sympatry with the described species (e.g., Marshall and West 2008; Ortiz 2008; Ortiz and Bertani 2014; Lapinski et al. 2018). On rare occasions taxonomy and ecology go hand in hand exploring possible segregation mechanisms (Prentice 1997; Bertani 2012). In genus revisions sometimes data concerning habitat or other natural history traits are included (e.g., Fukushima and Bertani 2017), but often species from the same genus are not sympatric (Bertani 2012).

Due to the paucity of ecological studies on local tarantula assemblages it is still impossible to infer patterns of their community ecology and test hypotheses regarding the driving mechanisms behind syntopy and sympatry that may apply to tarantulas. In general, for relatively mobile animals habitat selection may be an important factor (Morin 2011; Rao 2017). They may move among areas and actively choose where they forage, reproduce, or live. Thus, habitat choice may affect community patterns. Factors influencing habitat choice are the avoidance of physiological stress, competitors and enemies, as well as resource availability. For example, the avoidance of predators may result in the cost of reduced opportunities for foraging. Thus, when trying to understand and explain community patterns it is imperative to keep in mind that the patterns may result from animals making choices *before* becoming part of a community and from interactions at biotic and abiotic level *after* they became part of the community (Morin 2011). This calls for a multi-focus approach surveying local communities over longer periods of time instead of rapid assessments.

With respect to habitat use, Rao (2017) introduced the term topophilia arguing that although site selection in spiders depends on multiple factors, substrate characteristics are of primary importance followed by subsequent site evaluation (but see Lapinski and Tschapka 2014). Topophilia contains both behavioral and structural preferences of spiders. It is not static yet constrained and may change with changing conditions of the environment or ontogeny the individual. The author emphasizes the role of microhabitat structure and recognizes three levels of topophilia: (1) Macro level: habitat types and environmental characteristics; (2) Micro level: microhabitats, e.g., certain species or types of plants or soils; and (3) Nano level: certain structural features within microhabitats. Of course there exists some overlap between those levels. For example, *Eustala perfida* (Araneidae) occurred only inside of the forest on tree trunks of large trees with rough bark (Messas et al. 2014). Or *Avicularia* species (Theraphosidae) living in the Amazonian rainforest on tree trunks and in epiphytic bromeliads as well as on palm thatched huts (this chapter). If recent papers on tarantulas have any sort of habitat information they refer mostly to topophilia at macro level.

In the following, I summarize information on habitat use by New World Theraphosidae (Fig. 7.1). Most information was obtained from species descriptions and genus revisions and some from the few existing ecological studies. Additionally, I present a case study comparing the tarantula assemblages of the Sarapiquí region, Costa Rica and Río Napo, Ecuador with special focus on the arboreal lifestyle. Maps were created with QGIS 3.6 Noosa (available at www.qgis.org) using ESRI

Fig. 7.1 Approximate northern and southern distribution limits of New World Theraphosidae. Arrow indicates the introduced *Tliltocatl vagans* to Florida, USA

raster layer from OGS eb Map Service. Distributional information was added manually according to the information given in the respective publications dealing with the taxon in question.

7.2 USA: *Aphonopelma*

According to Hamilton et al. (2016), in the United States, 29 species of the genus *Aphonopelma* are distributed from west of the Mississippi River to California (but see Turner et al. 2018) (Fig. 7.1, Table 7.6). Additionally, *Aphonopelma* species occur in Mexico and Central America. The North American species of *Aphonopelma* live across a wide range of physical and climatic conditions from hot and arid regions near Death Valley (California, USA) to more temperate high-elevation forests along the Mogollon Rim and Madrean Archipelago (Arizona, USA). *Aphonopelma* species construct mostly silk-lined burrows in the ground and inhabit nearly every habitat throughout their distribution range where trees are usually scarce or completely lacking. Being fossorial, *Aphonopelma* species construct four burrows types: (1) "scrape" or burrow under rock in rocky habitats, (2) burrow with a turreted mound around the entrance, (3) burrow with a distinct crescent mound around the entrance, and (4) typical freestanding burrow without distinct mound around the entrance in desert, grassland, or rocky habitats.

The lineages within the *Paloma* species group are miniaturized species and are usually found in syntopy with a larger species (generally from the *Iodius* species group). Syntopy among members of the *Paloma* species group is rare. The larger *Aphonopelma* species usually are distributed beyond the distribution range of individual members of the *Paloma* species group. Body size frequently affects the niche of an organism (Hanken and Wake 1993) so that this miniaturization and the associated changes in niche utilization may have evolved as a consequence of ancestral character displacement (Hamilton et al. 2016). Thus members of the *Paloma* species group were enabled to use available microhabitats where the larger species were less abundant (Prentice 1997), allowing persistence in syntopy with larger taxa. As various species still are "problematic" in terms of identity, ecological differences among syntopic/sympatric species are difficult to assess. Syntopy among some *Aphonopelma* species has been documented with burrows sometimes in very close proximity (50 cm); in some cases sympatry is only assumed but not documented (Hamilton et al. 2016) but syntopy or sympatry analyses of the assemblages with respect to habitat use are lacking. So besides taxonomy there is still much to be learned about the ecology of North American tarantulas.

Prentice (1997) showed very nicely that the combination of taxonomy and the integration of quite detailed distributional and different life history data is well possible. He studied three sympatric *Aphonopelma* species from the Mojave Desert (USA): *A. iodius* and two significantly smaller species from the *Paloma* species group (*A. joshua* and *A. mojave*) (Fig. 7.2). All three species co-occurred only in the north-western part of the Joshua Tree National Monument. Since *A. joshua* and

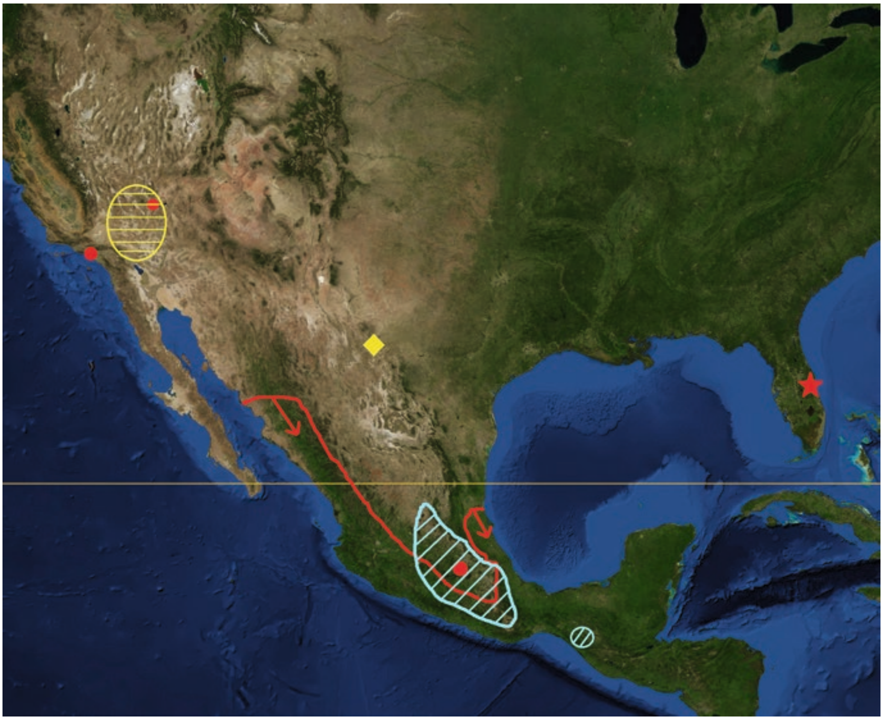


Fig. 7.2 Approximate distributions of some selected tarantula taxa. Yellow area: *Aphonopelma mojave*, *A. joshua*, and *A. iodius*, yellow diamond: study site *A. hentzi*. Red line: northern distribution limit of *Brachypelma* spp. in Mexico. Light blue areas: *Hemirrhagus* spp. Yellow dots: Las Vegas and Los Angeles (USA), Mexico City (Mexico). References: see the respective chapter paragraph

A. mojave had similar ecological requirements they were found in syntopy only in the before mentioned habitat. Both species placed their burrows in similar sandy soil of various particle size with similar vegetation communities. They occurred between 550 and 1600 m a.s.l. on flat or gently sloping terrain. *Aphonopelma iodius* in contrast was found at elevations between 300 and 1700 m a.s.l. and had higher tolerance to various soil types (rocky, clayey), and thrived in xeric conditions as well as in cooler and mildly hydric climates. Overall, Prentice (1997) showed that sympatric species may show differences in respective distribution ranges and specific tolerances of substrate quality and climate. Besides that syntopic species of similar body size and habitat use may differ in their hunting and breeding activity patterns. The study indicates the importance of integrated research reaching far beyond taxonomy. However, from that some questions arise: Why is *A. joshua* restricted to such a small area? How does habitat use of different instars differ intra- and interspecifically? At least in *A. mojave* the author found second and third year juveniles living together with the mother tarantula in its burrow.

Punzo and Henderson (1999) examined a population of *Aphonopelma hentzi* in the northern region of the Chihuahuan Desert (USA) (Fig. 7.2). The species occurred throughout this area. Adult females either excavated their own burrows or occupied burrows abandoned by rodents. Adult males sometimes occupied a burrow but were more frequently found within rock crevices or beneath rocks. The early instars were rarely observed and were typically found under rocks or dead vegetation in this area but were never found within a burrow. Larger juveniles rarely occupied burrows but seemed to prefer rock crevices and were sometimes found within crevices along the sides of rocky canyon walls up to 4 m off the ground. Temperature at the deepest point of the burrows was constant during the course of the day (ranging 26–29 °C), being significantly lower than surface temperature at early afternoon (59 °C) and slightly higher during the night. This shows the adaptive advantage of burrows in areas with extreme climate conditions. However, since juveniles apparently do not excavate burrows one might ask: How is the relationship between microclimate of typical shelters of juveniles and the ambient microclimate? Furthermore, as juveniles were found on canyon walls up to 4 m: How high were the walls and how is the vertical distribution of the juveniles? According to Hamilton et al. (2016) *Aphonopelma hentzi* is the most widely distributed tarantula species in the United States. The species inhabits a great variety of elevations and habitats including metropolitan areas and population density can be quite high. Depending on the habitat the tarantulas excavate free standing burrows or scrapes (i.e., burrows under rocks or wood). Although *A. hentzi* may be syntopic to several other *Aphonopelma* species throughout its distribution range not much is known with respect to interspecific differences in habitat use or other interactions. An interesting behavioral shift in association with change of habitat structure was reported by Smith (1994). In an area previously heavily grazed by cattle the grazing was reduced considerably. Consequently the grass height increased significantly and during mating season balloons of silk appeared above the entrances of the burrows of adult females of *A. hentzi*. The balloons were held in position by the grass strands. The function of these balloons was assumed to guide searching males to the females by their pheromones. This example shows how grazing animals may modify certain habitat features which in turn may affect the lives of small ground dwellers such as tarantulas. How does this apply to American bison habitats or the African savannas? Unfortunately this phenomenon has not been examined in greater detail *A. hentzi*.

7.3 México: *Brachypelma* and *Tliltocatl*

Brachypelma species have received considerable attention both from taxonomical and autecological perspective. Currently, 17 *Brachypelma* species are recognized as valid (World Spider Catalog 2020, but see Turner et al. 2018). However, the most recent revision on the genus splits it into *Brachypelma* (8 “red knee” species) and *Tliltocatl* (7 species, former “red rump” *Brachypelma*) (Mendoza and Francke 2020). Certainly the attractive appearance and the resulting popularity of

Fig. 7.3 The “red-knee” tarantula *Brachypelma hamorii*, female, dry forest, foothills of Sierra Madre del Sur, Colima, Mexico. Photo: Eddy Hijmensen

Brachypelma species in pet trade converted them into flagship species among tarantulas for spider enthusiasts and biologists, and even non-biologists. Popularity as pets and habitat destruction make *Brachypelma* and *Tliltocatl* species good model organisms for arthropod conservation. In Mexico two lineages of *Brachypelma* occur in a great variety of habitats (Fig. 7.2, Table 7.6). Along the Pacific coast several “red-knee” species of *Brachypelma* sensu stricto (after Turner et al. 2018) inhabit relatively small neighboring, slightly overlapping areas (Locht et al. 1999; Mendoza and Francke 2017) (Fig. 7.3). The “red-rump” *Tliltocatl* species ranges from Veracruz, Oaxaca, Chiapas, and the entire Yucatán peninsula southward to Costa Rica (Valerio 1980; Arisqueta-Chablé et al. 2010; Locht et al. 1999; Rudloff 2008). *Tliltocatl vagans* (Fig. 7.4) is the only species of the former *Brachypelma*, if not the only theraphosid species, of which several aspects of natural history traits were intensively studied by various researchers (see below). *Brachypelma* and *Tliltocatl* species are usually fossorial, but in *T. vagans* smaller juveniles live rather in rotten logs or beneath some sort of debris (Reichling 2003). However, since almost all of the studies on tarantula natural history were conducted on late instars it is unknown if it also is true for other species of the genus.

7.3.1 “Red-knee” Brachypelma

These species are distributed along the Pacific coast of Mexico with *B. emilia* being the northernmost species of the genus and *B. smithi* inhabiting the southernmost range of “red-knee” *Brachypelma* (Locht et al. 1999; West 2005a; Mendoza and Francke 2017). The most detailed account on habitat types and burrow placement in Mexican species of *Brachypelma* was given by West (2005a). According to West (2005a), dry thorn forest is inhabited by all *Brachypelma* species with the exception

Fig. 7.4 The "red-rump" tarantula *Tliltocatl vagans*, male left, female right, tropical lowland evergreen forest, Biosfera de Calakmul, Campeche, Mexico. Photo: Eddy Hijmensen

of *B. auratum* which occurs at higher elevations in topical deciduous forest and pine-oak forest. These forest types are inhabited also by *B. emilia* and *B. klaasi*. Most species are not restricted to pure forests but occur also in transition habitats and some live in cattle pastures. Usually the burrows are found beside some larger objects on the ground like logs, boulders or tree roots and the burrows are excavated underneath those objects. Some species may occur in sympatry where distribution range limits overlap (West 2005a; Mendoza and Francke 2017) but no data are available by what means the respective sympatric species share the habitat. Even less is known about other sympatric tarantula taxa and the ecology of local assemblages. At the Biological Station Chamela (Jalisco), for example, *Brachypelma klaasi* co-occurs with *Bonnetina cyanifemur*, *Magnacarina cancer*, and a species of *Aphonopelma* (Mendoza et al. 2016). Yáñez and Floater (2000) studied the spatial distribution and habitat preference of *B. klaasi* in more detail at Chamela Biological Station. The species occurs at elevations between 300 and 1400 m a.s.l. along the Pacific coast from Tepic, Nayarit in the north to Chamela, Jalisco in the south. The habitat at Chamela was tropical lowland deciduous forest on neutral sandy soils. Spiderlings were found in small holes in the ground, intermediate juveniles occupied temporary burrows and if later instars had encountered suitable sites they inhabited a permanent burrow for many years. Interestingly *B. klaasi* appeared to be a diurnal species being most active in the morning and in the early evening. The spiders adopted either the sit-and-wait strategy or searched actively for prey even climbing up to 2 m in the vegetation. Yáñez and Floater (2000) found that at a spatial scale all specimens combined were aggregated but not at lower scale. Burrow distance ranged between 3 and 257 m (mean = 103 m, n = 13) and many burrows were in south-western areas with low tree and canopy density. No specimens were found in the north-eastern areas of the reserve. Sometimes the spiders needed several square meters of soil for the construction of their elaborate burrows. The authors found high evening humidity (and the associated low evening temperature) to be the best predictor for burrow presence. This may be associated with the ecophysiology of *B. klaasi* allowing the spiders to be diurnal, at least at that site. When the sky remained overcast for several consecutive days, I have sometimes found females of the fossorial tarantula of *Stichoplastoris obelix* (Fig. 7.10d) in a sit-and-wait posture at their burrow entrances in a Costa Rican lowland rainforest (see below). The vegetation dwelling ctenids *Cupiennius coccineus* and *C. getazi* were also found quite often during such days outside of their shelters (pers. obs.). At that Costa Rican site habitat use of large wandering spiders was linked to desiccation resistance (Lapinski and Tschapka 2014). Thus, microclimate may affect both habitat use and activity patterns of spiders. Additionally, Yáñez and Floater (2000) found that the number of prey items was significantly positively related to abundance and species richness of plants around the burrow indicating that plants may indirectly affect habitat choice by this species. Some questions arise from the findings of Yáñez and Floater (2000). Are all instars of *B. klaasi* diurnal or is there a difference among instars? Is *B. klaasi* diurnal both in the dry and in the rainy season? Do the other sympatric tarantula species occur in the north-eastern areas at Chamela, where *B. klaasi* is absent, resulting in a “checkerboard” pattern of species occurrences (Morin 2011)? Does the desiccation resistance of *B. klaasi* differ from the other sympatric species resulting in a physiologically mediated segregation by activity time or by area and its microclimate? As mentioned above, nocturnal sympatric *Aphonopelma* tarantulas may differ in their activity patterns throughout the year (Prentice 1997). Medina Soriano (2006) found in Chiapas at exactly the same localities adults of *Cupiennius salei* (Ctenidae) only during the wet season while adults of *C. chiapanensis* occurred only in the dry season. In the present case of sympatric tarantulas at Chamela much work is still to be done in order to describe the tarantula assemblage and to be able to formulate any hypotheses explaining the mechanisms driving the coexistence of those species.

7.3.2 “Red-Rump” Tliltocatl

The species of that lineage occur around the southern and south-eastern distribution limits of the “red-knee” *Tliltocatl* (Locht et al. 1999; West 2005a). *Tliltocatl verdezi* inhabits dry thorn forests in sympatry with *smithi* (West 2005a). *Tliltocatl schroederi* was described from the Acapulco area being sympatric with *T. verdezi* (Rudloff 2003) and hence probably with *B. smithi*, too. *Tliltocatl kahlenbergi* has been described from the town area of Veracruz on the Caribbean coast (Rudloff 2008).

Since the arboreal *Psalmopoeus victori* was described from the rainforest in San Andrés Tuxtla (Veracruz) (Mendoza 2014b) it is possible that in Veracruz it co-occurs with either *T. kahlenbergi* or *T. vagans*, forming an assemblage consisting of at least one fossorial and one arboreal species.

According to Locht et al. (1999), *Tliltocatl vagans* occupies the entire southern part of Mexico. Furthermore the species is distributed all over Belize even on the dry cays offshore (Reichling 2003) and northern Guatemala (Hijmensen 2009). The species was introduced to Florida (USA) around 1986 (Edwards and Hibbard 2003). On the Yucatán peninsula *T. vagans* is sympatric with *T. epicureanum* (Arisqueta-Chablé et al. 2010) although their respective ecological differences have not been assessed yet. Similar to the above mentioned *Aphonopelma* species from the Mojave Desert (USA) (Prentice 1997) in addition to slight differences in habitat use one segregating mechanism of both *Tliltocatl* species might be the mating season. Most males of *T. vagans* were found in July and August whereas most males of *T. epicureanum* were collected in October (Arisqueta-Chablé et al. 2010). Hijmensen (2009) found in Calotmul on a recently burnt corn field three sympatric fossorial tarantula species: *Tliltocatl epicureanum*, *Crassicrus lamanai*, and *Aphonopelma* cf. *stoicum*. Various aspects of life history and ecology of the widely distributed *Tliltocatl vagans* were examined by several researchers during the last two decades. It is ecologically by far the most adaptive species of the genus thriving in a great variety of different habitats from tropical deciduous and tropical evergreen forest to cattle pastures, plantations, the respective transitional habitats, residential lawns, garbage dumps, and soccer fields (Reichling 2003; West 2005a; Machkour-M'rabet et al. 2005; Hijmensen 2009). In Campeche (Mexico) the species was not found in the interior of primary and secondary forests but preferred clearly rather disturbed sites, forming there very dense populations. This suggests that originally *T. vagans* inhabited open early succession areas being thus preadapted to inhabit anthropogenically modified habitats. However, within those anthropogenically disturbed areas, densities of adult females were more negatively affected by intensity of human activity than juveniles (Machkour-M'rabet et al. 2005). In Belize *T. vagans* was also strongly associated with highly disturbed areas living in dense populations. Shaw et al. (2011) report that at the clearing of the research station, which was surrounded by lowland tropical rainforest, more than 100 burrows of juveniles and adults were located over the course of two consecutive years. Individual specimens changed their burrow placement quite often. Regularly flooded areas had almost no burrows. In case of permanent burrows existing in such areas, the burrows were placed closely to objects (rocks, building edges, large roots) that stabilized the soil preventing the burrows from collapsing when inundated. The high adaptability of *T. vagans* to human activity was also reported by Hijmensen (2009). In Orange Walk Town (Belize) a whole colony was found in a hotel backyard. Another dense colony of *T. vagans* and *Crassicrus lamanai* was found on the lawn around the Mayan ruins at Lamanai. In the town of San Ignacio (Belize) close to the border with Guatemala every lawn was full of *T. vagans* of all instars, with spiderlings living in wall crevices and the larger instars in burrows (Hijmensen 2009).

Given the high adaptability of *Tliltocatl vagans* the species appears not to be in danger of extinction due to habitat loss. Au contraire, as anthropogenically modified habitats expand and connect (and pristine forests shrink getting isolated) *T. vagans* may benefit through both gaining suitable habitats and increasing gene flow among formerly isolated disturbed areas (Machkour-M'rabet et al. 2012). Thus *T. vagans* may function as a bioindicator of habitat degradation as proposed for the Argentine tarantula *Grammostola vachoni* by Schwerdt et al. (2018). However, other taxa, not being legally protected by CITES or otherwise, may face negative effects of habitat fragmentation and destruction. Clearly, much more work has still to be done in order to understand habitat use among syntopic and sympatric tarantulas and to being able to implement any protective measures in Mexico and elsewhere.

7.4 Exit Light, Enter Night: Cave Dwellers of Mexico, and Beyond

Caves are very special habitats. Apart from the entrance area the various effects of sunlight in deep caves are nil and climate inside the caves fluctuates little throughout the year. Caves may contain water bodies from small pools to subterranean rivers and in deeper regions of caves the chemical composition water may deviate quite strongly from the "normal" state outside caves. Besides that, caves are mostly very confined and isolated habitats. All this may lead to high endemism due to mostly impeded gene flow among populations. Every cave may have its particular conditions of abiotic factors resulting in unique cave-specific evolution of organisms living there (Culver and White 2005).

Beside species accounts there is virtually nothing known about any biological aspect of cave dwelling Theraphosidae. Most species were collected in extremely low numbers so that the few natural history data are very preliminary. Sixteen out of 27 *Hemirrhagus* species were collected only in caves 20–800 m from the entrance (Mendoza 2014a; Mendoza and Francke 2018, Fig. 7.5). Thus this is the only genus with epigean, troglophile, and troglobitic species. The known distribution range of *Hemirrhagus* is central to southern Mexico (Mendoza and Francke 2018) living thus in sympatry with other Mexican tarantulas (Fig. 7.2, Table 7.6). Cave-living *Hemirrhagus* species are segregated from other sympatric tarantulas by the obligatory cave-dwelling lifestyle. Within caves the spiders mainly occur on the floor and on walls, using rocks and crevices as shelters. While Mendoza (2014a) assumes *H. pernix* to occur in pine forest, Horstkotte et al. (2010) reports the species from the cave Cueva del Azufre. It lived in syntopy with large-sized araneomorphs (Ctenidae, Pisauridae) and Amblypygi. In a feeding experiment the *H. pernix* female consumed all four presented cave mollies that usually live in the toxic water of the cave.

Another new-world tarantula genus that contains both epigean and at least one troglobitic species is *Tmesiphantes*. Bertani et al. (2013) described *T. hypogeus* from two sandstone/quarzitic caves in the state of Bahia (Brazil), found on humid rocky substrates (Table 7.6). Dias et al. (2015) report on a relatively high density of theraphosids in a 150-m long "hot cave" in the state of Sergipe, also north-eastern Brazil. "Hot caves" are characterized by high temperatures and humidity maintained by dense populations of bats. In one case a *Lasiodora* species was observed consuming a bat on the cave floor and at least seven other tarantulas were in its vicinity (Table 7.6). Judging from the photograph the *Lasiodora* specimen belongs to an epigean species suggesting that epigean tarantula species may enter caves and stay there if conditions are favorable. This is also suggested by the encounter of

Fig. 7.5 *Hemirrhagus* sp., female, Mexico. Photo taken in captivity in the lab at UNAM, Mexico. Photo: Eddy Hijmensen

three unidentified tarantulas which lived in shelters among rocks just at the entrance of the "Río Frío" cave in the Mountain Pine Ridge, Belize (Hijmensen 2009). The presented cases show how little we know about caves as habitats for organisms in general and cave-dwelling tarantulas in particular. Caves certainly may become fruitful playgrounds for researchers that are eager to express their precious adventurer genes.

7.5 Brazil: Mata Atlântica

The habitats of north-eastern Brazil are a mixture of different vegetation zones: caatinga = seasonally dry tropical forest (Cardoso et al. 2017), restinga = strings of beaches and sandy dunes covered by herbaceous and arbustive-arboreal vegetation (Rocha et al. 2007), cerrado = Brazilian savanna encompassing open grassland to forest with a discontinuous grass layer (Oliveira and Marquis 2002), and of course the rainforest fragments along the Brazilian Atlantic coast. Due to this mosaic of heterogeneous habitats, which are connected by transitional areas or separated by habitats modified by man, the biodiversity is high and the region shows several zones of endemism with respect to Theraphosids (Bertani 2012). In those various biomes at least five vegetation-dwelling Aviculariinae genera have been recorded: *Avicularia*, *Ybyrapora, Iridopelma*, *Pachistopelma*, and *Typhochlaena* (Fig. 7.6, Table 7.6).

With an adult body length between 10 and 20 mm the currently five known *Typhochlaena* species belong to the smallest arboreal theraphosids and show the most deviating lifestyle among this subguild. The species inhabit the lowland Atlantic rainforest, the nearby restinga, and adjacent drier habitats caatinga and cerrado from Paraiba in the northeast to Espirito Santo in the southeast, and Maranhão and Tocantins further to the west (Bertani 2012; Andre and Hüsser 2016). All species were found on vegetation, under loose tree bark or under low leaves of bushes. In areas close to the forest, wandering males may occur also in houses searching for

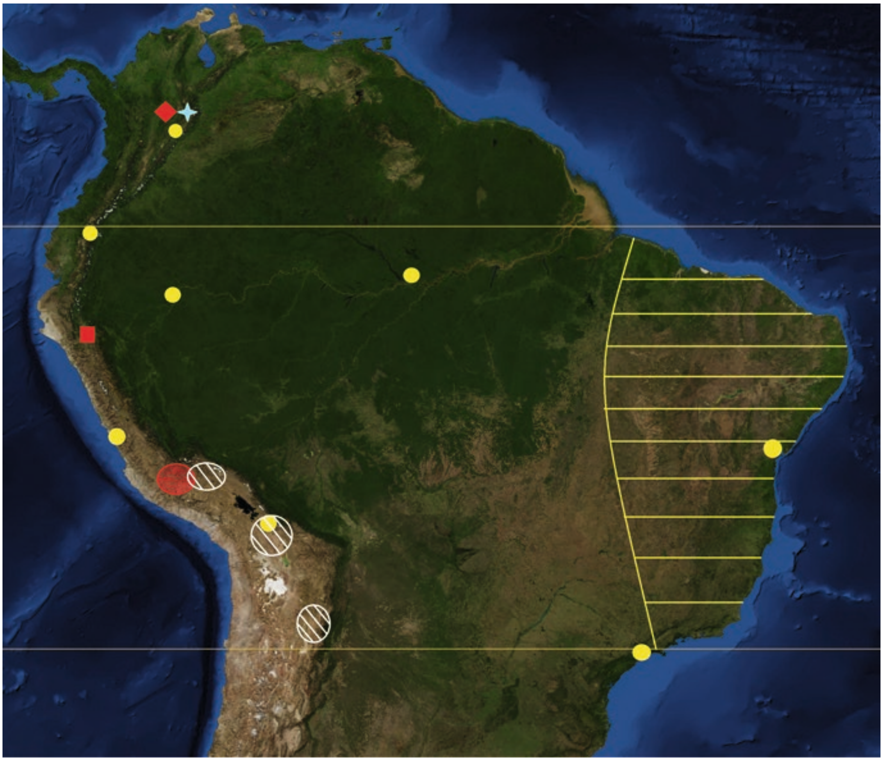
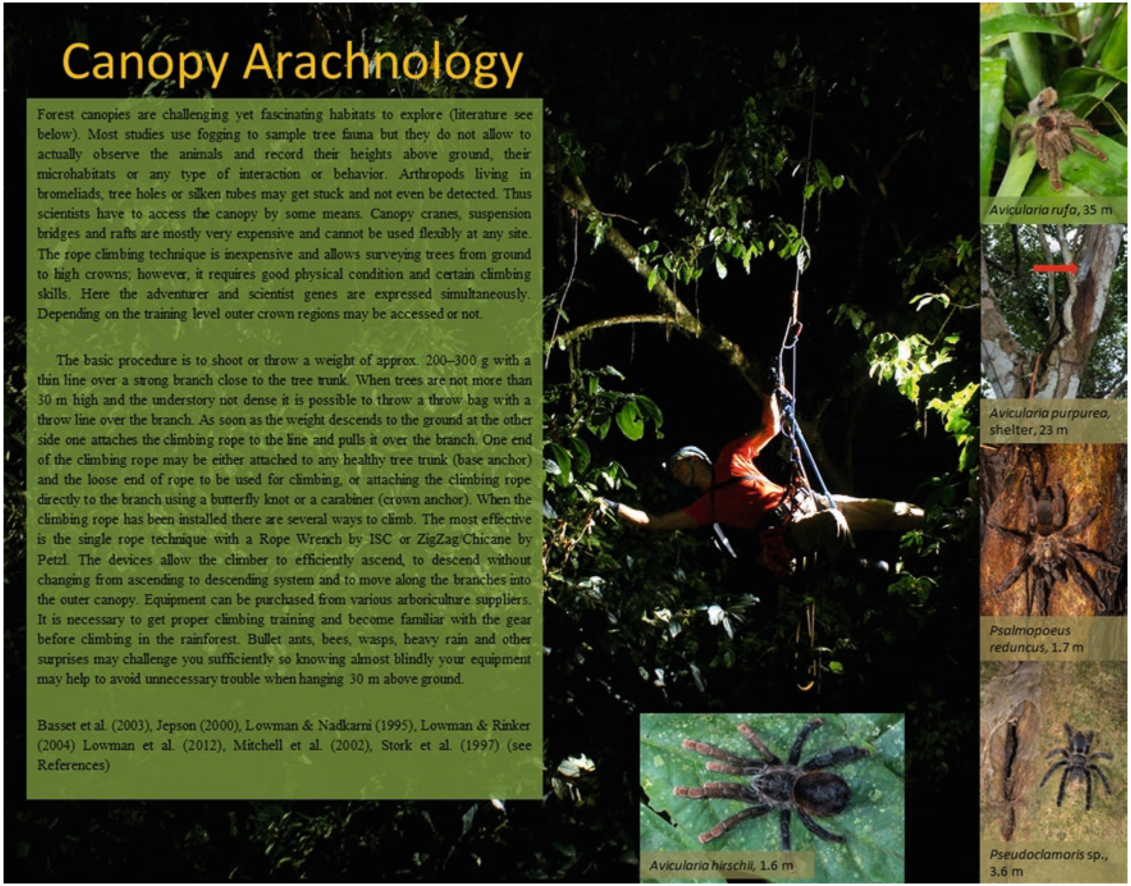


Fig. 7.6 Approximate distributions of some selected South American tarantula taxa. Red diamond: *Aguapanela arvi*, blue cross star: *Agnostopelma* spp., red square: highland *Cyriocosmus* spp., red circle area: *Bistriopelma* spp., white areas: *Hapalotremus* spp., yellow area: *Dolichothele* spp., *Ybyrapora* spp., *Iridopelma* spp., *Pachistopelma* spp., *Typhochlaena* spp., and a few *Avicularia* spp. Yellow dots anticlockwise: Bogotá (Colombia), Quito (Ecuador), Iquitos and Lima (Perú), La Paz (Bolivia), São Paulo, Salvador da Bahia, and Manaus (Brazil)

females. Unlike in other arboreal species the shelters of *Typhochlaena* species are very cryptic refuges that are rather short, located in a small hole or crevice in the bark covered by a trap door. Often the spiders rasp pieces of bark from inside of the shelter and include them into the silk of the trap door thus enhancing the camouflage effect (Almeida-Silva et al. 2008; Bertani 2012; Andre and Hüsser 2016). The miniaturization may have allowed those tarantulas to occupy such microhabitats (Hanken and Wake 1993). In a lowland rainforest area Andre and Hüsser (2016) found some shelters of *T. seladonia* with and without occupant in heights between 1.6 and 5.0 m above ground, in one case even three shelters on the same tree. The authors found *T. seladonia* in syntopy with *Ybyrapora diversipes* and *Iridopelma zorodes*. Due to the small body size and very secretive lifestyle of *Typhochlaena* species thorough ecological field research is quite difficult and it takes much patience and dedication to obtain useful data. Here surely the rope climbing technique (see below and info box) would help to assess more completely the three dimensional habitat use by these beautiful tarantulas.



Canopy Arachnology

Forest canopies are challenging yet fascinating habitats to explore (literature see below). Most studies use fogging to sample tree fauna but they do not allow to actually observe the animals and record their heights above ground, their microhabitats or any type of interaction or behavior. Arthropods living in bromeliads, tree holes or silken tubes may get stuck and not even be detected. Thus scientists have to access the canopy by some means. Canopy cranes, suspension bridges and rafts are mostly very expensive and cannot be used flexibly at any site. The rope climbing technique is inexpensive and allows surveying trees from ground to high crowns; however, it requires good physical condition and certain climbing skills. Here the adventurer and scientist genes are expressed simultaneously. Depending on the training level outer crown regions may be accessed or not.

The basic procedure is to shoot or throw a weight of approx. 200–300 g with a thin line over a strong branch close to the tree trunk. When trees are not more than 30 m high and the understory not dense it is possible to throw a throw bag with a throw line over the branch. As soon as the weight descends to the ground at the other side one attaches the climbing rope to the line and pulls it over the branch. One end of the climbing rope may be either attached to any healthy tree trunk (base anchor) and the loose end of rope to be used for climbing, or attaching the climbing rope directly to the branch using a butterfly knot or a carabiner (crown anchor). When the climbing rope has been installed there are several ways to climb. The most effective is the single rope technique with a Rope Wrench by ISC or ZigZag/Chicane by Petzl. The devices allow the climber to efficiently ascend, to descend without changing from ascending to descending system and to move along the branches into the outer canopy. Equipment can be purchased from various arboriculture suppliers. It is necessary to get proper climbing training and become familiar with the gear before climbing in the rainforest. Bullet ants, bees, wasps, heavy rain and other surprises may challenge you sufficiently so knowing almost blindly your equipment may help to avoid unnecessary trouble when hanging 30 m above ground.

Basset et al. (2003), Jepson (2000), Lowman & Nadkarni (1995), Lowman & Rinker (2004) Lowman et al. (2012), Mitchell et al. (2002), Stork et al. (1997) (see References)

Avicularia rufa, 35 m

Avicularia purpurea, shelter, 23 m

Psalmopoeus reduncus, 1.7 m

Pseudoclamoris sp., 3.6 m

Avicularia hirschii, 1.6 m

Pachistopelma bromelicola and *P. rufonigrum* occur more or less along the Atlantic coast of eastern Brazil from Rio Grande do Norte to Alagoas (*P. rufonigrum*) and from Sergipe to Bahia (*P. bromelicola*). Both species inhabit mostly terrestrial tank bromeliads, preferably exposed to direct sunlight. The habitats are mostly restinga, caatinga, and rainforest areas. In the latter case *P. rufonigrum* were found in terrestrial bromeliads on rocky outcrops, a rather hot and dry habitat compared to the surrounding rainforest. Such patches of bromeliads are quite separated from each other resulting in isolated populations. *Pachistopelma bromelicola* was also found in tank bromeliads used as ornamental plants in gardens. Bertani (2012) did not find any *P. bromelicola* in a rainforest area. However, do tank bromeliads occur there on trees in the canopy and could it be that the spiders just track the bromeliads up into the canopy? In general, large tank bromeliads may store water for a long time and organic matter may accumulate among the leaf axils; this is a good base for many arthropods, reptiles, and amphibians. They use the bromeliads for shelter, as water source and are feeding either on the accumulated organic matter or forage for prey living in the bromeliads. Even more than tank bromeliads of the rainforest canopy these plants are key for survival of many small animals in hot and otherwise dry habitats lacking the temperature and humidity gradient of a forest (Santos et al. 2003, 2004; Dias and Brescovit 2003, 2004; Bertani 2012; Lapinski and Tschapka 2014).

The genus *Iridopelma* is distributed from Pará in the west to Rio Grande do Norte and Bahia in the northeast. *Iridopelma hirsutum* and *I. zorodes* inhabit the rainforest fragments along the Atlantic coast, while the other four species occur farther west to Pará in drier habitats like cerrado and caatinga. Interestingly, *I. hirsutum* and *I. zorodes* make their retreats in a similar way connecting leaves with silk or inhabit bromeliads or rolled *Heliconia* leaves. The four species of the drier habitats were found occasionally similar to *Pachistopelma* spp. in terrestrial tank bromeliads but also under loose bark and, rather untypical for Aviculariinae, under fallen tree trunks and rocks. The greatest height at which *Iridopelma* spp. were found was 1 m above ground, which was certainly a bias of the survey method (Bertani 2012).

Ybyrapora species occur along the Atlantic coast of Brazil from Bahia southward to the state of Rio de Janeiro (Bertani and Fukushima 2009). *Ybyrapora gamba* is only known from Elísio Medrado near Salvador (Bahia) where it has been found in syntopy with *Y. diversipes* (Fig. 7.7); however, the latter species ranges farther southward along the Atlantic coast of Bahia. *Ybyrapora sooretama* occurs from the southernmost Bahia to southern Rio de Janeiro state. All three species are associated with the Atlantic rain forest, although the densest population of *Y. diversipes* was found in a secondary forest recovering for about 30 years from cocoa plantation. In a nearby experimental cocoa plantation the population was less dense. All three species constructed their shelters on tree trunks, large leaves and occasionally in tank bromeliads, similar to *Iridopelma zorodes* from the same region. The height of *Ybyrapora* specimens ranged from several centimeters to 2 meters above ground. According to the authors, *Y. gamba* constructed retreats also on grass (Poaceae), which also was reported for a juvenile specimen of *Avicularia hirschii* in Ecuador (Hüsser 2017).

Avicularia taunayi is the southernmost species of the genus in Brazil (Fukushima and Bertani 2017) and unlike its rainforest congeners it inhabits the cerrado located between Amazonia to its west and north, and Mata Atlântica to its east and south-east

Fig. 7.7 Juvenile of *Ybyrapora diversipes*, occurring in the Atlantic tropical rainforest region of north-eastern Brazil. Photo taken in captivity

(Bertani and Motta 2013) where *Typhochlaena*, *Pachistopelma*, *Iridopelma*, and *Ybyrapora* species occur (see above). The pristine cerrado and anthropogenically modified areas form a mosaic of habitats in that region. In this savanna-like region, *A. taunayi* live mainly on small trees which have relatively many holes in their trunks in which the spiders have their silken shelter tubes. The tarantulas have been found between 0.5 and 2 m above ground on the scattered trees. Similarly, Bullmer et al. (2006) found *Avicularia hirschii* on a pasture in Ecuador. Like *A. taunayi* the spiders inhabited scattered small trees with grass in between; however, I have found *A. hirschii* also in the Amazonian rainforest (see below).

Another theraphosid genus from north-eastern Brazil is *Dolichothele* (Guadanucci 2011). Judging from the distribution map presented by Guadanucci (2011), these Ischnocolinae are sympatric with some of the above mentioned Aviculariinae. *Dolichothele* species are terrestrial and at least one species, *D. bolivianum*, construct burrows strongly lined with camouflaged silk beneath stones and logs (Guadanucci 2007).

Sympatry: Syntopy in the Mata Atlântica

The complex habitat mosaic of the Mata Atlântica of north-eastern Brazil is inhabited by several tarantula species of which only the vegetation dwelling aviculariines have been examined in more detail. Bertani (2012) suggested that distribution ranges of most congeneric species are separated by major rivers in that region and that the Mata Atlântica shows various centers of endemism. As summarized above, those genera mainly use available plants in order to forage for prey and construct shelters, while species in forested areas live on trees and understory herbs, species of caatinga and restinga use the terrestrial tank bromeliads. Where species live in syntopy they are segregated by their lifestyle. For example, in one area of endemism between Rio São Francisco and Rio Paraguaçú the species *Iridopelma zorodes*, *Pachistopelma bromelicola*, and *Typhochlaena seladonia* are found in sympatry.

While *I. zorodes* lives in forested areas on trees and herbs, sometimes also in bromeliads, *T. seladonia* also lives on trees but constructs the trap-door retreats and uses small crevices in or under the bark. *Pachistopelma bromelicola* lives outside of forested habitats in tank bromeliads. For a more detailed analysis of biogeography of those genera see Bertani (2012). The question arises why *Pachistopelma* species specialized on terrestrial tank bromeliad in open habitats while sympatric *Iridopelma* species inhabit the vegetation of forested habitats Bertani (2012). To me the question is: are *Pachistopelma* species really restricted to open areas? In an attempt to explain the assumed segregation pattern Bertani (2012) suggests that large wet rainforest areas of the region were converted into xeric habitats due to climate fluctuations of the Neogene and the Quaternary periods. Because of their adaptations to hot and dry conditions of rainforest canopies bromeliads were preadapted to thrive on the ground of those xeric habitats providing valuable shelter and food resources for local fauna. Later the climate became humid again and some areas restored the forest character, but some remained xeric, forming a mosaic of forested and open habitats, all being inhabited by their specific faunas. However, the comparison of canopy with terrestrial bromeliads suggests that conditions among these regions may differ strongly (Gonçalves-Souza et al. 2010).

Exploring vertical transects from the forest ground to the canopy in the forested areas should reveal whether *Pachistopelma* species actually are restricted to tank bromeliads in open areas. Due to their assumed physiological adaptations to hot and dry environments, they might also thrive in the nearby forest canopy, not necessarily in epiphytic tank bromeliads, while *Iridopelma zorodes* and *I. hirsutum* be restricted to lower parts of the forests.

7.6 High Up on the Mountain

Tarantulas are of tropical origin and hence their basic physiology is adapted to temperatures between 20 and 30 °C and relatively high humidity. But there are exceptions to that. High up on the mountains, where clouds stroke their slopes, where calderas and glaciers almost meet tarantulas, the spiders face other challenges. The climate may be arid, semi-arid, or very humid with a wide range of temperatures. At an elevation of ca. 2000 m a.s.l. in the central Chilean Andes, for example, the air temperature can range from 0 to 40 °C, with surface temperature exceeding 60 °C (Alfaro et al. 2013). Snow may fall even in summer and during winter time the snow cover me be up to 3 meters (Cubillos et al. 2018). Records of tarantulas occurring at elevations above 2000 m a.s.l. are accumulating, yet not much is known about the habitat use of highland tarantulas. Physiological adaptations of South American tarantulas to cold were studied by Veloso et al. (2012), Alfaro et al. (2013), and Cubillos et al. (2018).

In the United States a few *Aphonopelma* species from the *Marxi* species group inhabit mountain ranges between 2000 and 2700 m a.s.l. mainly in oak woodland, pine-oak woodland, and mixed conifer communities of northern Arizona and New

Mexico (Table 7.6). The biology of highland tarantulas in the United States is poorly known; the burrows or shelters of *A. chiricahua*, for example, have not even been observed yet. In *A. madera* only one scrape burrow has been observed, all other males and females were observed walking around during day time while all juveniles occurred under stones without any burrows (Hamilton et al. 2016). In Mexico, epigean species of the genus *Hemirrhagus* live in cold climate zones between 1500 and 3100 m a.s.l. and can be found mainly in pine, oak, or pine-oak forest (Mendoza 2014a) (Table 7.6).

The highest elevation records for New World theraphosids are from the Andes (Fig. 7.6, Table 7.6). In Colombia *Agnostopelma tota* and *A. gardel* occur at approximately 3000 m a.s.l. in shelters under stones, nothing more has been reported about those species (Pérez-Miles and Weinmann 2010). Another Colombian highlander is *Aguapanela arvi* from the Piedras Blancas Ecological Park between 2100 and 2400 m a.s l., which take shelter in rock crevices and inhabit high Andean cloud forests (Perafán et al. 2015). According to the authors, the park with recovering cloud forest is an area of high diversity of Mygalomorphae; other sympatric theraphosids are *Hapalopus* sp. and *Ami* sp. The authors report also, based on museum material, that in Colombia there are also highland species from the genera *Catumiri* (2004 m a.s.l.) and *Holothele* (3000 m a.s.l.). Even less is known about highland tarantulas from Ecuador; all known species were described from the mountain ranges around Quito: *Cyclosternum gaujoni* from elevations between 2600 and 3600 m a.s.l. (Berland 1913), *C. schmardae* from 4000 to 5000 m a.sl. (Peters 2005 citing Ausserer 1871), *Pamphobeteus augusti* from forests on Pichincha volcano and *P. vespertinus*, both occur at approximately 2800 m a.s.l. (Pocock 1903; Peters 2003). In Peru species from at least three genera can be termed highlanders. Pérez-Miles and Weinmann (2009) described from northern Peru *Cyriocosmus pribiki* and *C. rogerioi* inhabiting cloud forests at elevations between 2200 and 3000 m a.s.l. In the southern Andes of Peru, two species of *Bistriopelma* and six species of *Hapalotremus* were discovered at even greater elevations. *Bistriopelma lamasi* and *B. matuskai* live at elevations between 3749 and 4398 m a.s.l. on grass slopes in burrows under stones and rocks. The average annual temperature ranges from 9.5 to 11.2 °C and may reach 0 °C (Kaderka 2015). Slightly to the south-east of their distribution range six species of *Hapalotremus* inhabit the high Peruvian Andes at elevations between 2500 and 4524 m a.s.l.; this is to date the highest elevation for any theraphosid and the record goes to *H. vilcanota*—if the above mentioned elevation range of *Cyclosternum schmardae* in the Ecuadorian Andes not be verified. Peruvian *Hapalotremus* species were found both in burrows and in crevices under rocks while ambient temperature may fall well below 0 °C (Ferretti et al. 2018). The distribution of *Hapalotremus* continues southward to Bolivia and north-western Argentina. In the Bolivian Andes two *Hapalotremus* species inhabit the edges of Yungas at elevations between 3200 and 4252 m a.s.l. In north-western Argentina *H. martinorum* occurs in high Andean cloud forest at around 1500 m a.s.l. and *H. chasqui* lives in the grass land with tree groves at 1300–2000 m a.s.l. Here the temperatures vary between as high as 26 °C in summer and 16 °C in winter, often reaching −10 °C (Ferretti et al. 2018).

Four highland *Euathlus* species occur from northern to central Chile at elevations from 1900 to 3200 m a.s.l. living in semi-arid habitats where temperatures may drop well below 0 °C (Veloso et al. 2012; Alfaro et al. 2013; Perafán and Pérez-Miles 2014; Cubillos et al. 2018). In northwestern Argentina *E. diamante* inhabits semi-arid grass and shrub land at 2200 m a.s.l. Two more species live even further south at lower elevations between 1042 and 1400 m a.s.l. in small crevices and short burrows under stones in the Patagonic steppe (*E. sagei*) and in quite humid Andean-Patagonic forests (*E. tenebrarum*) (Ferretti 2015). Veloso et al. (2012) found that *Euathlus parvulus* (central Chilean Andes) may select shelter sites (rocks) that have certain climatic regimes, which in combination with temperature in the deeper burrow allow the spiders to thermoregulate behaviorally.

7.7 Costa Rica and Ecuador: Local Assemblages Compared

7.7.1 Methods

In the light of a tremendous paucity of comparative studies at assemblage level, often even lacking basic natural history data I present a case study with ecological data collected mainly in the Sarapiquí region, Costa Rica and compare this assemblage to that found in the Oriente of Ecuador (Fig. 7.8, Table 7.6).

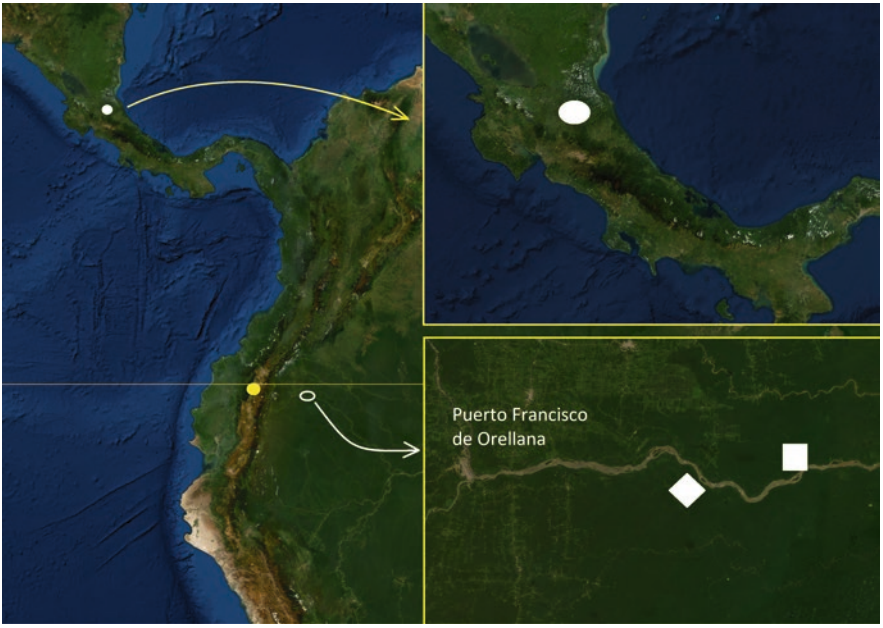


Fig. 7.8 Study sites in Costa Rica (white dot: Sarapiquí region) and Ecuador (white circle: along Río Napo). Yellow dot: Quito (Ecuador). Detailed location of the study sites along Río Napo (Ecuador): Centro de Interpretación Yaku Kawsay (white diamond) and Sani Lodge (white square)

I used the World Spider Catalog (version 21.0) to obtain information about total number of described Theraphosidae species from both Costa Rica and Ecuador. Then I assigned the known species to two subguilds: (1) terrestrial and (2) arboreal in order to compare the proportion of both lifestyles in Costa Rica and Ecuador.

Methods Costa Rica

On several short trips and long-term stays I collected data on basic tarantula ecology in Puerto Viejo de Sarapiquí (March 2001), at Reserva Biológica Tirimbina (August 2006 to June 2007, April to July 2008, and March 2010 to March 2012), the banana plantation of Chiquita Finca Nogal and a nearby forest fragment Agrícola Sofía were surveyed monthly from November 2010 to March 2012. The banana plantation of Finca Guayacán and the forest of Refugio Nogal were visited sporadically when visiting Finca Nogal and Agrícola Sofía. Tarantula species were identified using Valerio (1979–1980), Pérez-Miles et al. (2008) and comparing them to the specimens deposited at the Museo de Zoologia, Universidad de Costa Rica. Alcohol and still living specimens are in the private collection of the author. *Neischnocolus panamanus* specimens are deposited in the Staatliches Museum für Naturkunde Karlsruhe, Germany (Lapinski et al. 2018) and in the private collection of the author.

Study Areas The sites were located in the Sarapiquí region at elevations between 40 and 220 m asl, Heredia Province, Costa Rica (Fig. 7.8). Mean annual temperature is 25.3 °C and mean annual precipitation is 3777 mm. (1) Puerto Viejo de Sarapiquí is a small town at approximately 50 m a.s.l. surrounded by a mosaic of fragments of lowland rainforest, banana plantations, pastures, and and other agroecosystems. To its south there is La Selva Biological Station and the northernmost part of Braulio Carrillo National Park. (2) Refugio Nogal is a small temporarily inundated rainforest fragment at Río Sucio with its understory formed by many *Heliconia* plants. South to it there were (3) the banana plantations of Chiquita: Finca Guayacán and Finca Nogal. The plantations formed together an area of approximately 390 ha and according to Chiquita staff agrochemicals were used only moderately. The banana plants were 3–4 m tall, interspersed with few herbs. The ground was covered by cut banana plants and banana leaves. (4) To their west there is the rainforest fragment Agrícola Sofía of approximately 176 ha with infrequent logging activity. (5) Reserva Biológica Tirimbina (RBT) has an area of approximately 345 ha and is located approximately 16 km south-west of Puerto Viejo de Sarapiquí at an elevation between 180 and 220 m a.s.l. About 85% of the reserve's forest is classified as primary forest, encompassing also areas of secondary forest of various age classes. Canopy height at the forest study sites ranged between 30 and 40 m, with emergent trees up to *ca* 50 m. For a more detailed description of RBT see Lapinski and Tschapka (2013, 2018).

Fieldwork Most fieldwork at all sites was conducted by walking trails during day and night turning objects on the ground, searching for tarantula burrows in the ground and for shelters on all plants up to approximately 4 m, and for active tarantulas. At RBT there are two suspension bridges allowing canopy surveys up to approximately 26 m. However, closer inspection of tree trunks, epiphytes, and trees holes was very restricted. Therefore I used single rope technique (Jepson 2000;

Barker and Standridge 2002; see info-box) between September 2010 and February 2012 to repeatedly survey 22 trees belonging to 12 different species once per month (hereafter called vertical transects, details see Lapinski and Tschapka 2018). As spiders usually are not host-tree specific I surveyed suitable trees from different species (Sørensen 2003 and references therein). Selection criteria of suitable trees were: accessibility by the arrow shot from the ground in order to install the climbing rope and height at least that of the surrounding canopy. Spiders were searched at night on trunks and central portions of the crown of each tree individual and its surrounding vegetation from ground to approximately 3 meters above the branch where the rope was attached to. Data were taken within a survey radius of approximately 5 meters around the rope-climbed tree and only during the ascension to prevent repeated sampling. Prior to ascension spiders were also searched for 15 min on the forest ground, on the lower tree trunk and on understory vegetation within a 5-meter radius around the rope-climbed trees to collect also data on spiders roaming the lower strata of the forest. Spiders of all but the smallest instars were searched during 152 surveys of varying duration, from 1830 to 0415 h, the exact starting hour depended on weather conditions. Surveys on tall and structurally more complex trees usually took longer than on smaller and less complex trees, also the number of actual encounters prolonged the survey duration. Spiders at greater distance from the climbing observer were identified using binoculars (Pentax 8x36 DCF HS). It was never observed that spiders fled when illuminated by head lamp; sometimes they retreated into their shelters when vibrations caused by the climber's movements were too strong.

Methods Ecuador

Study Areas Data on basic tarantula ecology were collected between November 13 and 24, 2017 at two sites along the Río Napo at an elevation of approximately 200 m a.s.l. (Fig. 7.8). The landscape has slightly undulating hills (terra firme), lower parts of rainforest close to Río Napo and its larger tributaries are flooded seasonally (igapó). Mean temperature in the region ranges between 24 and 28 °C and annual rainfall is between 2800 and 3000 mm. The study sites were approximately 30 km apart: (1) Centro de Interpretación Yaku Kawsay run by the Kichwa community Nueva Providencia located along Río Shipati, close to its mouth into Río Napo. The community has an area of 6426 ha and lies in the most north-western part of Yasuní National Park, Orellana Province. The Yasuní National Park has a total area of approximately 1,022,736 ha. The site has secondary and primary lowland rainforest and swamps inside the forest and along the river. On the clearing there were five traditional huts with palm thatched roofs, no insecticides were used. The huts were connected by elevated wooden walkways, in between there were some small fruit trees and the ground was covered by short grass. (2) Sani Lodge is run by the Sani Isla Kichwa community and is located north of Río Napo at the lake Challuacocha. In the cabins and other facilities of the lodge insecticides were applied, the soil of clearing was covered by short-cut grass. Around of and in the vicinity to Challuacocha there are several swamps. The rainforest is classified mainly as primary. An approximately 35 m high observation tower at a Kapok tree

(*Ceiba pentandra*) of approximately 45 m total height allows access to its crown and the epiphytes on its branches. The mainly uninterrupted rainforest north of Río Napo continues northward into Reserva de Producción de Fauna Cuyabeno, resulting in a vast continuous lowland rainforest. Canopy height was approximately 30 m with emergent trees up to 50 m.

Fieldwork The procedure was similar to that applied in Costa Rica. Due to the short stay two trees of unknown identity were climbed at Yaku Kawsay. At Sani Lodge one still living tree clasped by a well-developed strangler-fig was climbed and the canopy observation tower was also used to search for tarantulas in the crown of a Kapok tree (*Ceiba pentandra*) of more than 45 m total height. *Avicularia* species were identified using Fukushima and Bertani (2017) by habitus and two exuviae, *Neischnocolus yupanquii* by habitus using Pérez-Miles et al. (2008), and *Megaphobema velvetosoma* by habitus by the dedicated tarantula aficionado A. Stirm who knows this species well. Three other tarantula species were assigned to morphospecies based on completely different habitus, i.e., physical appearance and coloration. Besides two *Avicularia* exuviae no specimens were collected.

Variables and Statistical Tests During the surveys I collected the following data: date, hour, individual number, species, instar, sex, site, habitat type, microhabitat—which I later subdivided into topophilia at micro- and nano-scale (Rao 2017)—shelter type, height of spider above ground, and diameter of plants, trunks, twigs, etc. where a spider was perching on, and tree species when possible. At RBT I also assessed the following structural variables of the rope-climbed trees: diameter (usually in breast height), total tree height, relative height of lowest branch (=height of lowest branch/total tree height). The amount of epiphytes on the trunk, amount of epiphytes within the crown, number of holes in the trunk, and number of holes within the crown were estimated and subdivided into classes. Epiphyte classes were: 1 = few (≤20% cover), 2 = many (ca 20–50%), 3 = almost full (≥50%), hole classes were: 0 = none, 1 = some, 2 = few, 3 = many. I used SigmaStat (Version 3.5) for all analyses. Continuous non-normally distributed data were analyzed with Kruskal–Wallis one way ANOVA on ranks using Dunn's *post-hoc* test for unequal sample size. This test was used to examine whether (a) sympatric/syntopic tarantula species, (b) different instars of the Costa Rican arboreal *Psalmopoeus reduncus* differed in their vertical distribution, and (c) whether the diameter of plants/parts of plants used by *P. reduncus* differed among instars. To simplify the analysis of differences among instars I assigned them into the following instar classes according to their body length: large ≥3 cm, intermediate =1.6–2.9 cm, and small ≤1.5 cm. I used the Mann–Whitney Rank Sum Test to compare surveys from ground only with surveys along vertical transects in order to examine whether the survey method may affect the picture of vertical distribution in arboreal tarantulas. To do so, I analyzed height data of the arboreal *Psalmopoeus reduncus*, for which sample size is biggest. I created to groups (1) ground-only with height data up to 4 m which may be obtained easily from the ground (trails and ground collected data at vertical transects), and (2) vertical transects only with height data obtained only at the rope-climbed trees from ground to the highest point possible (survey details are described above).

In order to explore which structural tree variables may affect vertical distribution of *Psalmopoeus reduncus* I calculated relative height of spider = height of spider/ total height of the tree on which it was encountered. I used only the data obtained on the actually rope-climbed trees because structural characteristics of neighboring vegetation were not assessed. The data were $\log_{10}(x + 1)$—transformed, and then additionally standardized to omit mathematical problems caused by different units of different variables (Leyer and Wesche 2007). I used only the standardized data for further analyses. Relative height of spider was the dependent variable and the above mentioned tree variables were independent variables which first were entered into stepwise forward regression to identify those which may predict relative height of spider. With the identified predictor variables I ran a multiple linear regression.

7.7.2 Results

Comparison of Tarantula Lifestyle in Costa Rica and Ecuador

Ecuador has a surface area approximately 5.5 times that of Costa Rica but from the latter approximately 1.8 times more tarantula species were described. However, in Ecuador 8 out of 21 known species—or 38%—from four genera are arboreal, in Costa Rica there is only one well-documented arboreal species out of 37 reported species (3%) (Fig. 7.9). In Ecuador only one arboreal species (*Psalmopoeus ecclesiasticus* Pocock 1903) is known from the forests west of the Andes, the other genera and species occur east of the Andes ranging eastward well into the lowlands of Amazonia. Additionally, during the survey in Ecuador I found another arboreal, previously not reported species, resulting in a total of 9 arboreal out of 22 reported species (41%).

Costa Rica During the surveys from 2001 to 2012 the total of 104 individual tarantulas from five genera and five species were found (Table 7.1, Fig. 7.10). Most species were strongly associated with forest (forest interior and gaps in the forest) (Table 7.2). *Lasiodora icecu* occurred also in anthropogenically modified habitats, but both habitats were very close to the surrounding rainforest at RBT. Only one tarantula specimen, an adult male of *Stichoplastoris obelix*, was found in a banana plantation approx. 300 m from the forest fragment Refugio Nogal where a conspecific adult female was encountered.

Psalmopoeus reduncus occurred significantly higher than *Neischnocolus panamanus*, *Lasiodora icecu*, *Stichoplastoris obelix*, and *Sericopelma silvicola* (Fig. 7.11, Kruskal-Wallis ANOVA, $H_4 = 77.72$, $P \leq 0.001$, post hoc test Dunn's method $P < 0.05$). The greatest height recorded for *P. reduncus* was 28 m above ground (relative height = 0.72). The adult female had its shelter in a big tree hole among epiphytes. Median relative height in *P. reduncus* was 0.13 (vertical transects only). Exceptional heights in the terrestrial tarantula species were measured in a

Fig. 7.9 Comparison of the total number of Theraphosidae described from Ecuador and Costa Rica and the proportion of arboreal (green) to terrestrial (dark red) tarantula species recorded from those countries. Red bars represent country area in 10^3 km^2

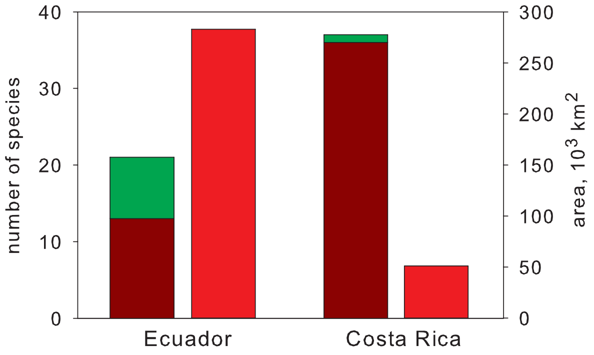


Table 7.1 Theraphosid species and sample size encountered at the different sites in the Sarapiquí region, Costa Rica

Species	N (RBT)	N (other)
Neischnocolus panamanus (Petrunkevitch 1925)	12	0
Lasiodora icecu (Valerio 1980)	11	0
Psalmopoeus reduncus (Karsch 1880)	54	1 AS
Sericopelma silvicola (Valerio 1980)	13	1 PV
Stichoplastoris obelix (Valerio 1980)	10	1 FG, 1 RN
N (total)	100	4

RBT Reserva Biológica Tirimbina, other include, *AS* Agrícola Sofía, *FG* banana plantation Finca Guayacán, *RN* Refugio Nogal, *PV* sec. Forest in Puerto Viejo de Sarapiquí

female *N. panamanus* found on a trunk of *Vochysia guatemalensis* in 1.4 m, where it retreated under loose bark during capture attempt. Two females of *L. icecu* had their burrows in 1.4 and 1.6 m on a 2-m high and almost vertical embankment of an unpaved road. The burrows of those two females were 20 cm apart.

In order to examine whether the survey method may influence the picture of vertical distribution of arboreal *P. reduncus*, I compared data on "height of spiders above ground" obtained at vertical transects (i.e., searching from ground around the rope-climbed trees and during actual climbing those trees) with height data obtained only from the ground by walking trails and by searching on and around rope-climbed trees from ground only (data from both canopy bridges were omitted because such bridges are, like ropes, a type of technical canopy access system). The height above ground of *P. reduncus* was significantly greater at fully surveyed vertical transects than in ground-only surveys, resulting in documented occurrence up into the canopy region of the rainforest and higher median of height at which *P. reduncus* may occur (Fig. 7.12, Mann–Whitney Test, $T = 949.00$, $n(\text{small}) = 22$, $n(\text{big}) = 40$, $P \leq 0.001$).

To examine whether there exist ontogenetic habitat shift in the arboreal *P. reduncus* I tested for differences among three instar classes with regard to (1) height above ground and (2) diameter of plant parts on which specimens were found. The different instars of *P. reduncus* did not differ significantly in their height above

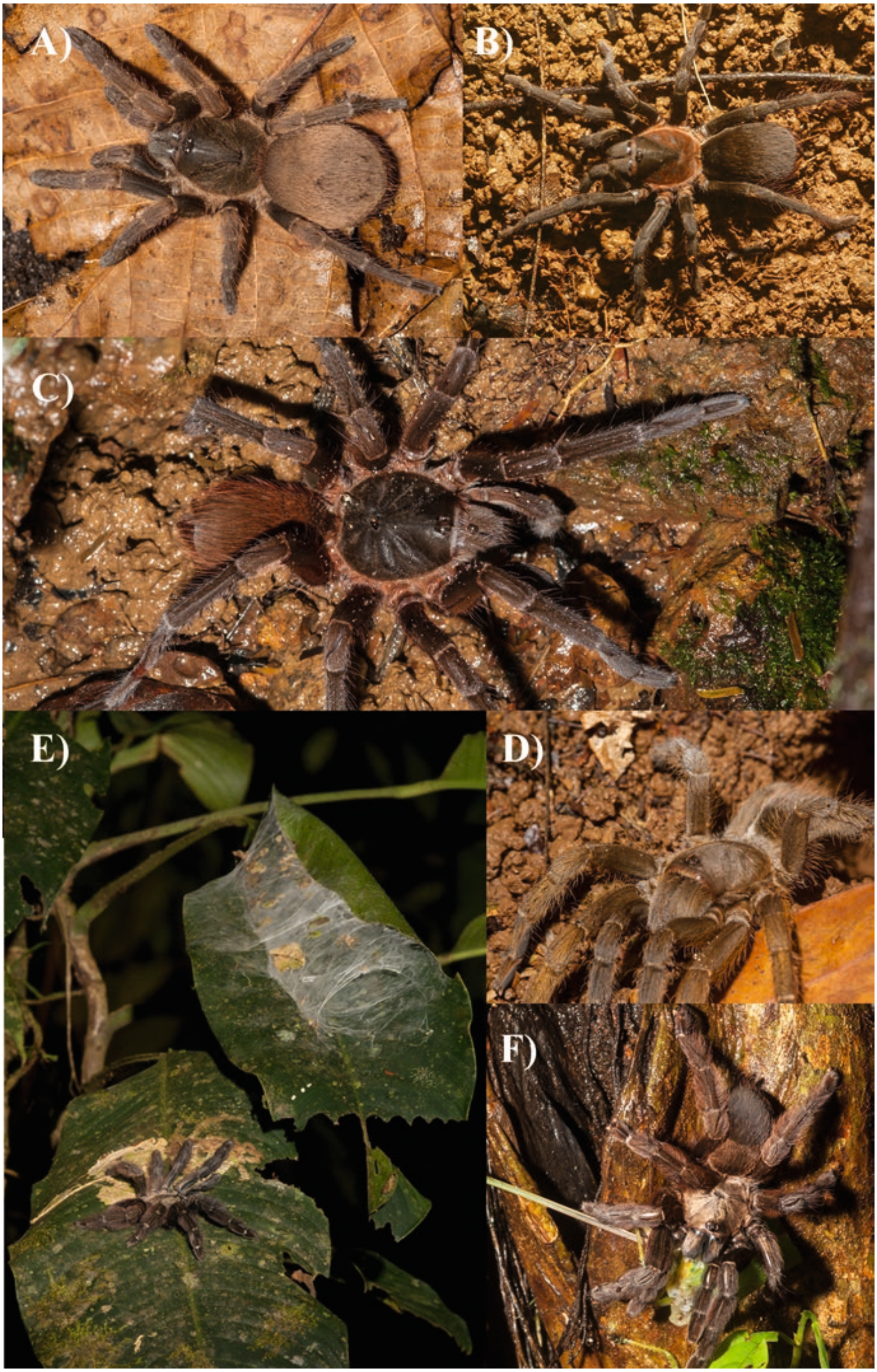


Fig. 7.10 Females of tarantula species from Reserva Biológica Tirimbina, Sarapiquí region, Costa Rica. (**a**) *Neischnocolus panamanus*, (**b**) *Lasiodora icecu*, (**c**) *Sericopelma silvicola*, (**d**) *Stichoplastoris obelix*, (**e**) *Psalmopoeus reduncus* with silken tube on a *Philodendron* leaf, (**f**) *Psalmopoeus reduncus* as mostly found on tree trunks, here with a recently captured *Copiphora* sp. (Tettigoniidae)

Table 7.2 Habitat types used by the theraphosid species in the Sarapiquí region, Costa Rica

Species	Forest interior	Gap	Open area	Cacaotal	Banana pl.
Neischnocolus panamanus	11	1	0	0	0
Lasiodora icecu	8	0	2	1	0
Psalmopoeus reduncus	44	10	0	1	0
Sericopelma silvicola	13	0	0	0	0
Stichoplastoris obelix	9	2	0	0	1

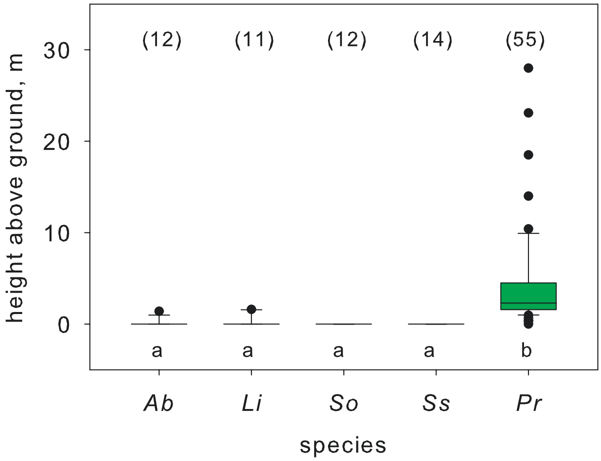


Fig. 7.11 Vertical distribution of the sympatric theraphosid species encountered at several study sites in the Sarapiquí region, Costa Rica. Data from both ground-only and vertical transect surveys pooled. Different letters below the boxes indicate significant differences, figures in parentheses above 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. Species abbreviations: Np = *Neischnocolus panamanus*, Li = *Lasiodora icecu*, So = *Stichoplastoris obelix*, Ss = *Sericopelma silvicola*, Pr = *Psalmopoeus reduncus*

ground (Fig. 7.13a, Kruskal-Wallis ANOVA, $H_2 = 2.28$, $P = 0.32$). Although a significant difference in diameter of plants or their parts used by *P. reduncus* was found only between large instars and spiderlings (Fig. 7.13b, Kruskal-Wallis ANOVA, $H_2 = 12.92$, $P = 0.002$, post hoc test Dunn's method $P < 0.05$), overall large and intermediate instars tended to use plants with greater diameter than spiderlings.

Topophilia In the Costa Rican assemblage there was a conspicuous segregation of the species by topophilia at micro scale (Fig. 7.14). Ground and trail banks were used almost exclusively by *L. icecu*, *S. obelix* and *S. silvicola*; *N. panamanus* was not found on banks. Vertical objects, mostly trees, were occupied by *P. reduncus*. There was almost no overlap among the two subguilds at that scale, with the exception of a wandering male of *P. reduncus* on the ground and the above mentioned female of *N. panamanus* on a tree trunk. Figure 7.15 shows segregation of topophilia at nano scale. *Psalmopoeus reduncus* mainly used structures associated with plants. But there was also segregation among the terrestrial species. While *L. icecu*,

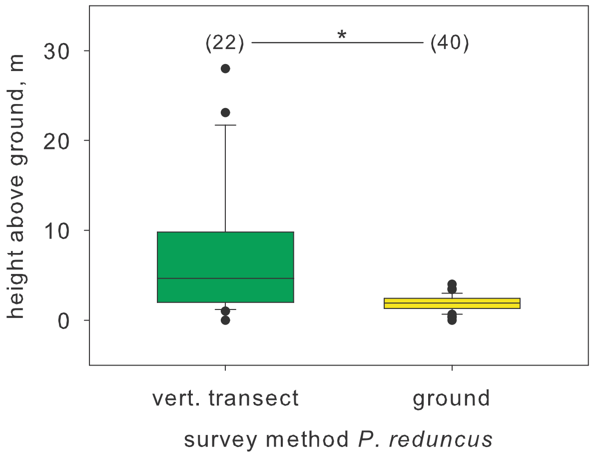


Fig. 7.12 Comparison of the effect of survey method on resulting picture of vertical distribution of the arboreal *Psalmopoeus reduncus* in Costa Rica. The asterisk indicates significant difference, figures in parentheses above the boxes show sample size. Horizontal lines in the boxes represent the median, boxes are from Q_{25} to Q_{75}, error bars from Q_{10} to Q_{90}, full circles are outliers

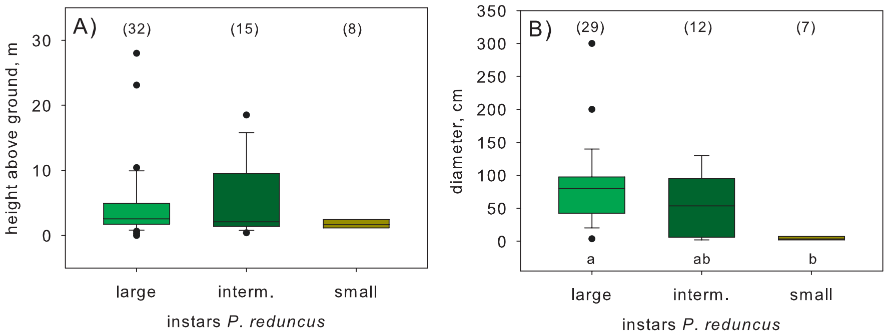


Fig. 7.13 Comparison of three different instar classes of the arboreal *Psalmopoeus reduncus*. (**a**) Height above ground, and (**b**) diameter of plant parts the specimens were found perching on. Instar classes of the tarantulas: large ≥3 cm, intermediate = 1.6–2.9 cm, and small ≤1.5 cm body length. 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

S. obelix and *S. silvicola* were found mostly in or at burrows in the ground, *N. panamanus* occurred predominantly under wood or wandering around among leaf litter. Besides that a few wandering males of all but *S. silvicola* were found without being associated tightly with a certain topophilia.

During the vertical-transect surveys the arboreal *Psalmopoeus reduncus* occurred on seven tree species with different structural characteristics. The tree species were: *Alchorneopsis floribunda* (Euphorbiaceae), *Ceiba pentandra* (Malvaceae-Bombacoideae), *Pentaclethra macroloba* (Fabaceae-Mimosoideae), *Terminalia*

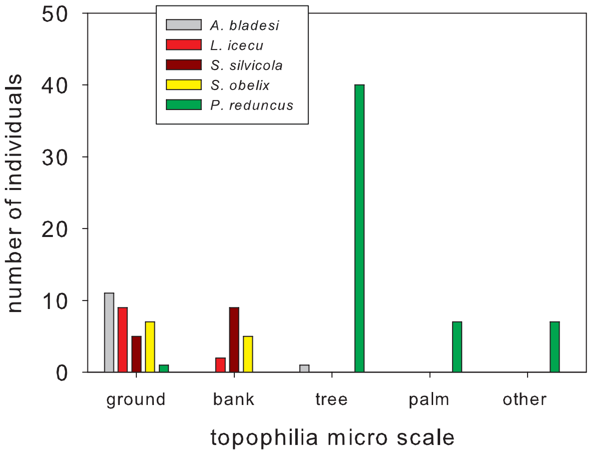


Fig. 7.14 Topophilia at micro scale of tarantulas found in the Sarapiquí region, Costa Rica. Other include: shack, hollow rail of stairs of a suspension bridge, log on ground, liana

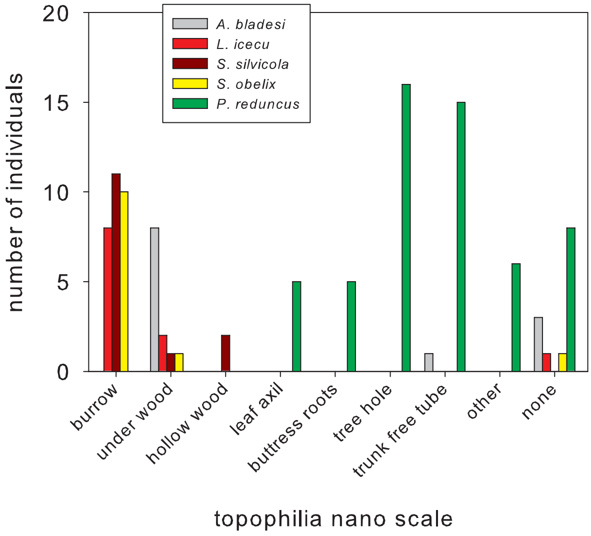


Fig. 7.15 Topophilia at nano scale of tarantulas found in the Sarapiquí region, Costa Rica, showing the placement of shelters. Other include: under roof of a shack, root of *Socratea*, leaf epiphyte. * *Neischnocolus panamanus* female on tree trunk, which retreated under loose bark when disturbed, but no silken structures were found

oblonga (Combretaceae), *Vitex cooperi* (Lamiaceae), *Vochysia guatemalensis* (Vochysiaceae), *Virola koschnyi* (Myristicaceae), and *Socratea* sp. (Arecaceae).

Relative height of the arboreal *Psalmopoeus reduncus* increased significantly with both the amount of epiphytes and amount of holes in the tree crowns (multiple linear regression, Table 7.3). The other assessed structural variables DBH, total tree

Table 7.3 Results of multiple linear regression analysis of relative height of n = 19 *Psalmopoeus reduncus* as dependent variable on n = 10 trees from 7 species and the independent variables trunk diameter, total tree height, relative height of lowest branch, amount of epiphytes on the trunk, amount of epiphytes within the crown, number of holes in the trunk, and number of holes within the crown

	Coefficient	Std. error	t	P	VIF
Constant	9.17E-16	0.13	7.11E-15	1	
Epiphytes in crown	0.72	0.14	5.27	<0.001	1.07
Holes in crown	0.29	0.14	2.15	0.047	1.07
Analysis of variance					
	DF	SS	MS	F	P
Regression	2	12.94	6.47	20.45	<0.001
Residual	16	5.06	0.32		
Total	18	18	1		
R = 0.85	$R^2 = 0.72$	Adj $R^2 = 0.68$			
SE of estimate = 0.56					

For definitions and details of variables see methods

height, relative height of lowest branch, and both amount of epiphytes on tree trunks and amount of holes in tree trunks did not add to the ability of the equation to predict relative height in *P. reduncus*. Greatest heights of *P. reduncus* were measured on *Vitex cooperi* (HS = 14–28 m, three spiders) and on *Ceiba pentandra* (HS = 18.5 m, one spider). Both trees were very tall and densely covered with epiphytes of different types from ground to crown. *Vitex cooperi*, however, had in addition to its epiphyte abundance more holes in the wood in the crown than *C. pentandra*. And exactly deep in a large hole an adult female of *P. reduncus* was found at the greatest height (28 m) in that *V. cooperi* tree. Although many of the surveyed trees in Costa Rica were heavily loaded with tank bromeliads up to 1 m in diameter on the trunks and on branches I never found any arboreal tarantula in a tank bromeliad.

Ecuador

I have found a total of 30 tarantula individuals at both sites in the Oriente of Ecuador belonging to nine genera and species (Table 7.4, Fig. 7.16). Apart from one intermediate juvenile of *Neischnocolus yupanquii* and one spiderling of *Megaphobema velvetosoma* and *Pseudoclamoris* sp., respectively, no small juveniles were found. Hence no data on possible ontogenetic habitat shift are available. Although I was not able to assign the three unidentified Theraphosinae species to any genus, their coloration and habitus differed sufficiently to treat them as different morphospecies belonging to different genera. Theraphosinae 3 is already known in the internet as Yasuní Tiger Tarantula and I use this name hereafter. The species is allegedly in the process of description but no further information is available to me. Yaku Kawsay and Sani Lodge shared only two species: *Megaphobema velvetosoma* and *Avicularia rufa*. However, due to the short time spent at both sites and hence small sample size these results have to be regarded only as preliminary.

Most species were restricted to the forest interior (both primary and secondary) (Table 7.5). Theraphosinae 1 and Theraphosinae 2 were only found on the clearing with huts at Yaku Kawsay. *Avicularia rufa* was found in the forest interior at Sani

Table 7.4 Theraphosid species and sample size encountered at the different sites along Río Napo, Ecuador

Species	N (YK)	N (SL)
Neischnocolus yupanquii (Pérez-Miles et al. 2008)	0	1
Megaphobema velvetosoma (Schmidt 1995)	1	4
Theraphosinae 1	4	0
Theraphosinae 2	1	0
Theraphosinae 3 (Yasuní Tiger Tarantula)	1	0
Avicularia hirschii (Bullmer et al. 2006)	0	1
Avicularia purpurea (Kirk 1990)	0	4
Avicularia rufa (Schiapelli and Gerschman 1945)	8	2
Pseudoclamoris sp. (cf. *burgessi*, Hüsser 2018)	0	3
N (total)	15	15

YK Centro de interpretación cultural Yaku Kawsay, *SL* Sani Lodge

Lodge, at Yaku Kawsay it occurred at forest edge along the bank of Río Shipati and on palm thatched roofs of the huts.

At both sites in Ecuador there were conspicuous differences in vertical distribution among the encountered tarantula species (Fig. 7.17). However, the sample size per species was too small to run a sensible ANOVA in order to examine interspecific differences in height of the spiders. Therefore, I subdivided all typically terrestrial (*Neischnocolus yupanquii* to Yasuní Tiger Tarantula) and all typically arboreal (*Avicularia hirschii* to *Pseudoclamoris* sp.) species into two corresponding groups: terrestrial versus arboreal. Mann–Whitney Test corroborated that the terrestrial species occurred at significantly lower heights than the arboreal ($T = 79.00$, $n(\text{small}) = 12$, $n(\text{big}) = 18$, $P \leq 0.001$). On the same tree/strangler fig-complex at Sani Lodge one adult female of *Pseudoclamoris* sp. (at 1.0 m) and three subadult/adult females of *A. purpurea* (at 10.1 m, 10.7 m, and at 23 m) were found.

The tarantula species were segregated with respect to topophilia at micro level (Fig. 7.18). The terrestrial species were obviously associated with ground; however, while *N. yupanquii* and *M. velvetosoma* occurred on the ground of primary and secondary forest, Theraphosinae 1 and Theraphosinae 2 were found on ground that was strongly modified by human activity (law and bare soil among and under the huts at Yaku Kawsay). The arboreal species were mainly associated with trees in primary and secondary forest, only *A. rufa* occurred also on manmade structures at Yaku Kawsay. The only specimen of Yasuní Tiger Tarantula, a female, was found in the rainforest understory.

Nano scale topophilia of the theraphosids found at both sites was quite diverse (Fig. 7.19). Among the terrestrial species *M. velvetosoma* and Theraphosinae 1 lived mainly in burrows, *N. yupanquii* was wandering among leaf litter, Theraphosinae 2 was wandering on bare soil and Yasuní Tiger Tarantula was perching on a leaf of an understory Marantaceae, but no shelters of the latter three specimens were discernible. The arboreal species showed an even more diverse topophilia at nano scale. *Avicularia hirschii* lived in a silken tube on a horizontal leaf of a sapling and a dead leaf was attached to the upper side of the tube. *Avicularia purpurea* lived in mainly exposed silken tubes on trees, usually ending in a tree hole or crevice between tree

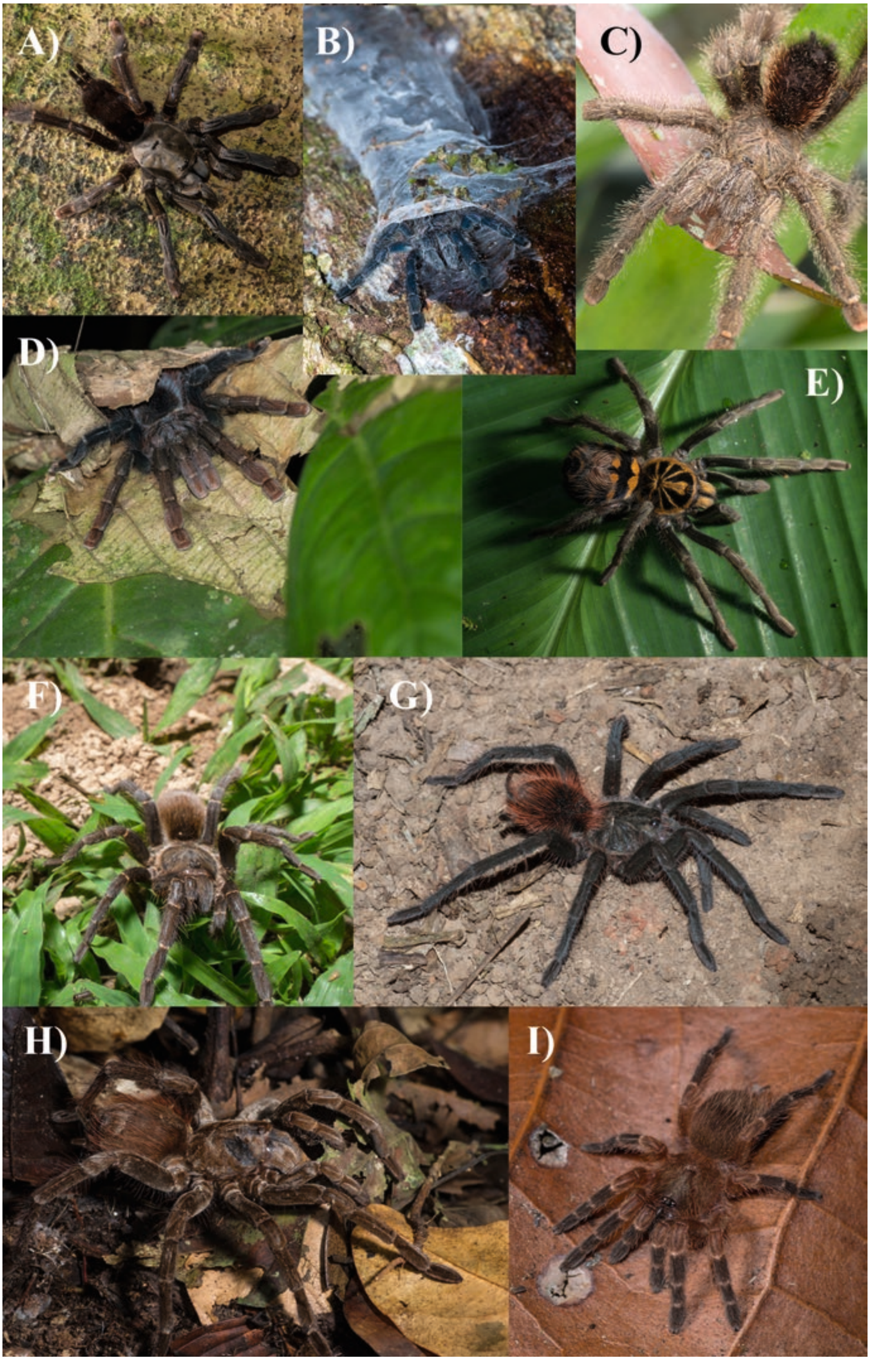


Fig. 7.16 Tarantula species from Yaku Kawsay and Sani Lodge, Río Napo, Ecuador. (**a**) *Pseudoclamoris* sp., (**b**) *Avicularia purpurea*, 23 m above ground, (**c**) *Avicularia rufa*, 35 m above ground, (**d**) *Avicularia hirschii*, (**e**) Theraphosinae 3 (Yasuní Tiger Tarantula), (**f**) Theraphosinae 1, (**g**) Theraphosinae 2, (**h**) *Megaphobema velvetosoma*, (**i**) *Neischnocolus yupanquii*, juvenile

Table 7.5 Habitat types used by theraphosids at Yaku Kawsay and Sani Lodge, Ecuador

Species	Forest interior	Forest edge	Clearing huts
Neischnocolus yupanquii	1	0	0
Megaphobema velvetosoma	5	0	0
Theraphosinae 1	0	0	4
Theraphosinae 2	0	0	1
Theraphosinae 3 (Yasuní Tiger Tarantula)	1	0	0
Avicularia hirschii	1	0	0
Avicularia purpurea	4	0	0
Avicularia rufa	2	2	6
Pseudoclamoris cf. *burgessi*	3	0	0

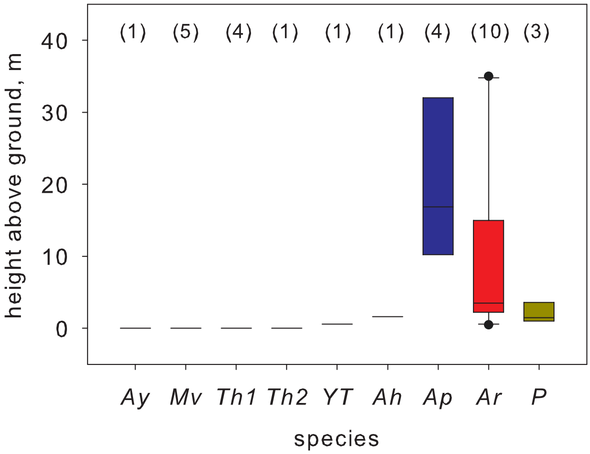


Fig. 7.17 Vertical distribution of the sympatric theraphosid species at Yaku Kawsay and Sani Lodge, Ecuador. Figures in parentheses above the boxes show sample size. Horizontal lines in the boxes represent the median, boxes are from Q_{25} to Q_{75}, error bars from Q_{10} to Q_{90}, full circles are outliers. Species abbreviations: Ny = *Neischnocolus yupanquii*, Mv = *Megaphobema velvetosoma*, Th1, Th2 = Theraphosinae 1 and 2, YT = Yasuní Tiger Tarantula (Theraphosinae 3), Ah = *Avicularia hirschii*, Ap = *Avicularia purpurea*, Ar = *Avicularia rufa*, P = *Pseudoclamoris* sp.

trunk and a strangler fig. However, an exuvia of an intermediate juvenile *A. purpurea* was found in a silken tube between the lateral leaves of a huge tank bromeliad 35 m above ground on a branch of a *Ceiba pentandra* of more than 45 m total height; but the occupant was absent. In the same tree crown two *A. rufa* females were found in those tank bromeliads without constructing a significant silken tube. Additionally at Yaku Kawsay, permanent silken tubes were inhabited by a female in a tree hole and by an intermediate juvenile on the board underside of a wooden walkway connecting the huts. The other specimens of *A. rufa* were found on the roofs of palm thatched huts. Interestingly, conspicuous and firm silken tubes were usually not built by *A. rufa* that occurred on those roofs and in the above mentioned bromeliads. Two rather loose silken sacks with fresh exuviae were found on the undersides of the palm thatched roofs, but the recently molted females roosted

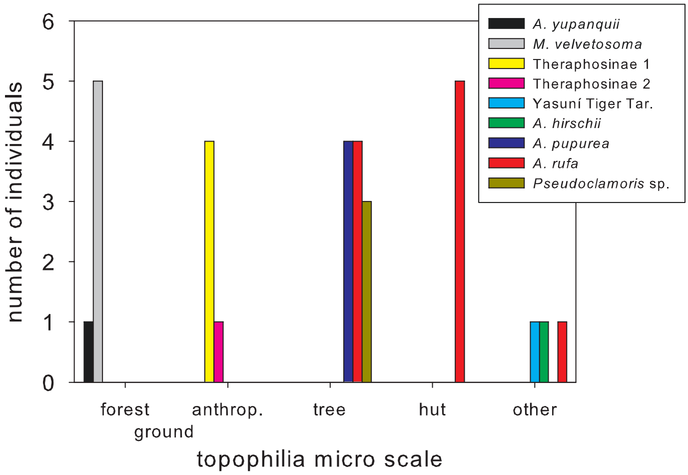


Fig. 7.18 Topophilia at micro scale, showing the microhabitat types used by the sympatric theraphosids at Yaku Kawsay and Sani Lodge, Ecuador. Other include: sapling (*A. hirschii*), wooden walkway (*A. rufa*, juv.), understory herb (Yasuni Tiger Tarantula)

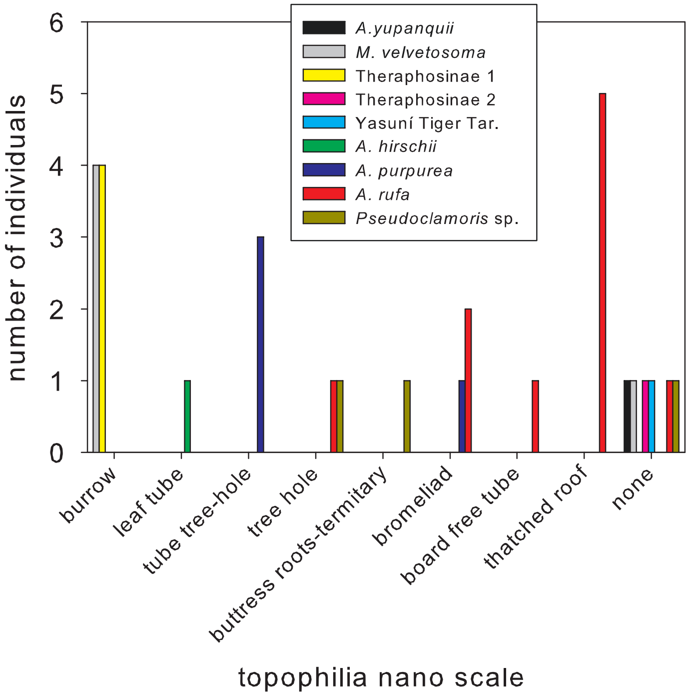


Fig. 7.19 Topophilia at nano scale of sympatric theraphosids at Yaku Kawsay and Sani Lodge, Ecuador, showing the placement and type of shelters

among nearby the palm leaves each day at a different location of the same roof. *Pseudoclamoris* sp. was found only on tree trunks. The spiderling was wandering freely at day upward and both adult females had their silken tubes in a tree hole and in a hole between a buttress root and an active termite nest (tree/strangler fig-complex).

7.7.3 Discussion

Basic Lifestyles of Tarantulas in Costa Rica and Ecuador

When comparing the known Costa Rican and Ecuadorian tarantula species with respect to the basic life styles terrestrial and arboreal, a difference or gradient in the proportion of arboreal to terrestrial habit between both countries and within Ecuador became apparent. The proportion in arboreality in Costa Rica is much lower than in Ecuador. In Ecuador itself the highest proportion of arboreality is found in the Amazon lowlands ranging into the eastern mid-elevations of the Andes, dropping dramatically within Ecuador when the Andes are crossed. This gradient is too conspicuous to be a random phenomenon. Seasonal flooding of vast areas affects many aspects of life in the Amazon basin (Adis 2002; Junk 1997; Kelly et al. 2017). Canopy arthropods are more sensitive to forest type than to biogeography (Basset 2001). The rainforest areas that were originally covering Central America and the Pacific lowlands of Ecuador with only small to intermediate-sized water bodies without pronounced inundations seem to not strongly promote arboreality. In Pantanal regular large-scale flooding influenced changes in both structure and composition of arthropod communities on trees (Marques et al. 2006). In contrast to Costa Rica and the Pacific lowlands of Ecuador, the Amazon basin with its seasonal interaction of forest with large-scale flooding and a mosaic of different terra firme and inundation forest types may drive and sustain high proportion of arboreality in arthropods in general and tarantulas in particular. From there arboreality might spread into surrounding biomes, decreasing in proportion with decreasing degree of seasonal large-scale floodings.

Tarantula Assemblages

Here I present a case study on the habitat use of two tarantula assemblages in the Sarapiquí region of Costa Rica and the middle Río Napo of Ecuador. Overall there was a general similarity in assemblage structure. In both study areas the respective assemblage consisted of several terrestrial and one (Costa Rica) to four (Ecuador) arboreal tarantula species, of which *Pseudoclamoris* sp. seems to be the first record for Ecuador. In both assemblages the terrestrial subguild contained one small species of the genus *Ami* and several intermediate to large species. While species of *Ami* usually take shelter under objects on the forest floor (mostly wood) instead of constructing permanent burrows (Auer 2011; Lapinski et al. 2018) the other terrestrial Theraphosinae mostly occupied burrows in the ground, only few individuals were found wandering on the ground or low in the understory. In Ecuador one arboreal and one fossorial species appear to tolerate or even prefer anthropogenically modified habitats. The facility area at Yaku Kawsay where three species occurred was small, still closely surrounded by rainforest and no insecticides were used. At Sani Lodge no tarantulas were found at the clearing and on the cabins despite proximity to the rainforest. Insecticides are used there and may explain the absence of tarantulas on the main facility area. However, just few meters into the surrounding secondary forest I found four tarantula species. Flexibility in habitat use, including the use of buildings, was also reported for other arboreal tarantulas, e.g., *Avicularia purpurea* from Tena, Ecuador (Kirk 1990) and *A. avicularia* from Trinidad (Stradling 1994). Despite frequent short-term and one long-term stay in Costa Rica, only two females of *Lasiodora icecu* were found along an unpaved road close to rainforest at RBT and only one adult male of *Stichoplastoris obelix* was found in a banana plantation. Weinmann (2003) examined a plantation with mixed crops in Colombia. He found a population of the fossorial *Megaphobema robustum* with an exceptional high density of 225 individuals/ha. A fossorial *Pamphobeteus* sp. shared this habitat, but no further data were given. In Martinique the arboreal *Caribena versicolor* was associated with forest areas and also occurred on nearby buildings but was usually absent from cultivated areas including banana and pineapple plantations (Maréchal et al. 2009). Thus, all five species found during the surveys in Costa Rica appear to be strongly associated with rainforest, rendering them vulnerable to forest destruction by man. In the studied Ecuadorian species at least two of them showed a sufficient degree of adaptability to anthropogenic habitat modification but certainly more thorough studies are needed. The difference in the proportion of arboreal to terrestrial species between the two studied Ecuadorian sites (4:2 at Sani Lodge, 1:4 at Yaku Kawsay) appears to be an artifact of the short survey time at each site. The only study to my knowledge that examines an assemblage of New World theraphosids was conducted in the Loreto region, Peru by Reátegui-Suárez et al. (2014). Like in Ecuador the region around Loreto is seasonally inundated (Auer 2011). At two sites five terrestrial species were encountered. Similar to the Ecuadorian assemblage presented here the authors found *M. velvetosoma* and *N. yupanquii*. In addition the Peruvian assemblage contained *Cyriocosmus sellatus*, *Pamphobeteus petersi*, and *Acanthoscurria ferina*. In Loreto again *N. yupanquii* was the only not fossorial and together with *C. sellatus* the smallest species. Strangely no arboreal species were found, or at least not reported. Only the fossorial species were analyzed in more detail, omitting *N. yupanquii*. The fossorial species placed their burrows in shaded places of the forest interior on slightly inclined relief with not dense understory vegetation and leaf litter of intermediate thickness. The burrows of different species were often only few meters apart.

Vertical Distribution

To my knowledge this is the first study that explores the ecology of theraphosids from forest ground to high rainforest canopy and at the same time includes data on syntopic species. The surveys in Costa Rica and Ecuador revealed a clear segregation of sympatric tarantula species by height above ground, forming a terrestrial and a vegetation-dwelling or arboreal subguild. The results show that arboreal tarantula species may use most of the available height range from low understory to high canopy as high as 35 m above ground as long as sufficient shelter possibilities exist. These results are in accordance with the vertical distribution of an assemblage of large wandering spiders sympatric with the tarantula assemblage at Reserva Biológica Tirimbina, Costa Rica (Lapinski and Tschapka 2013, 2018). During the tree surveys using rope climbing data on vertical distribution of both wandering spiders and tarantulas were collected simultaneously. Although overlapping in vertical distribution, the arboreal theraphosid *Psalmopoeus reduncus* occurred somewhat lower (median = 4.7 m) than the arboreal ctenid *Cupiennius coccineus* (median = 12.9 m). Knowledge of arboreal arthropods is strongly affected by survey methods (Basset 2001). Höfer et al. (1994) used fogging to sample the forest canopy in central Amazonia but not even one specimen of the frequently observed *Avicularia* sp. or other arboreal mygalomorph was collected. According to Valerio (1979) the Costa Rican arboreal *Psalmopoeus reduncus* lives in tree holes up to 4 m above ground. As shown here the species occurs frequently also in greater heights up to 28 m constructing silken tubes with different exposure degree. The comparison of ground-only surveys with surveys along vertical transects showed nicely that the survey method may affect the picture of the vertical distribution and topophilia of arboreal arthropods. The use of a canopy access system (observation tower and rope climbing) proved also to enhance the detection probability of arboreal species, since during the short stay at Sani Lodge I was able to find *Avicularia rufa* (tower) and *A. purpurea* (using both rope climbing and tower) only above 10 m, i.e., not visible from the ground. In addition, those methods facilitated direct observations of the animals, study of their shelters and all this without any necessity to kill them. The fun factor of studying the rainforest canopy in general and using the rope climbing technique in a beautiful tropical rainforest in particular cannot be neglected, either.

Ontogenetic Habitat Shift

Intraspecific differences in habitat use among different instar stages are common in various animal taxa and may reduce intraspecific competition and/or predation of juveniles by older, hence bigger, instars (reviewed by Morin 2011). Marshall and West (2008) found such ontogenetic habitat shift in the tarantula *Ephebopus murinus* in French Guiana, with small juveniles living in terrestrial bromeliads and larger to adult instars being fossorial. Due to the usually low population densities of tarantulas in rainforests in particular (pers. obs.), but also of many other spiders in general (Wise 1993), both intra- and interspecific competition and intraguild predation appear to be of little importance among rainforest theraphosids. In fossorial species small juveniles should be well protected from larger individuals by (a) low population density, (b) the predominantly sessile lifestyle, so that encounters are quite unlikely, and (c) by the small diameter of their burrows, into which a larger conspecific cannot follow easily. However, in the fossorial colonial *Tliltocatl vagans* females may enter burrows of conspecific females resulting in aggressive interactions among similarly sized individuals which are actually able to enter the burrows (Dor et al. 2008). Thus following *homo homini lupus* similar-sized instars in sessile tarantulas should be of greater danger to each other than distinctly bigger for smaller instars. Consequently, Marshall and West (2008) propose for *E. murinus* that the observed ontogenetic habitat shift might have evolved due to the evolutionary history where the fossorial habit may have evolved secondarily from arboreal life style. Within the genus *Ephebopus* a range from predominantly fossorial to rather arboreal species is documented (Marshall and West 2008; West et al. 2008). With respect to the “typically” arboreal tarantulas, West (2005b) reports a reversed ontogenetic habitat shift where size of plants and height of spiders may increase with instar stage. Data from the relatively large sample size of the Costa Rican arboreal *Psalmopoeus reduncus* suggest that this species does not exhibit any ontogenetic habitat shift in vertical distribution and only a slight in plant size expressed by diameter of object the spider was found on. However, the syntopic large ctenid *Cupiennius coccineus* showed a significant difference vertical distribution among three instar classes, with smaller instars occurring at greater heights (Lapinski and Tschapka 2018).

Topophilia at Micro and Nano Levels
At micro level tarantulas from the studied assemblages were associated either with ground (terrestrial species) or with vertical objects, mostly plants (arboreal species), both inside and outside of the rainforest. At nano level the encountered terrestrial species may be subdivided into fossorial species and species living under various objects on the ground (both *Ami* spp.). Microclimate inside of tarantula burrows in the ground stays constantly favorable compared to the outside microclimate (Punzo and Henderson 1999; Striffler 2005). This protective feature of burrows explains why only fossorial species were found on both ground and on banks of trails and roads both inside and outside of the surrounding forest. *Ami* species do not construct burrows (Auer 2011; Lapinski et al. 2018) and hence both *Ami* spp. were found on forest ground covered with leaf litter and wooden debris, avoiding clearings and the mostly bare soil of trail banks. The ecology of the Yasuní Tiger Tarantula (Theraphosinae 3) is completely unknown but inferring from its habitus it is most probably a ground-dwelling species. In Costa Rica and in Ecuador the studied arboreal species showed high variability in topophilia. At micro level topophilia ranged from plants of different types to buildings. At nano level the arboreal species not only used almost the entire available height range (see vertical distribution) but even within same species different parts of plants and buildings were used ranging from free silken tubes on trunks, silken tubes ending in tree holes or being placed almost completely to completely in tree holes. The data suggest that vertical distribution of the arboreal tarantulas may be positively correlated by structural complexity of host trees. In the large ctenid *Cupiennius coccineus* a similar effect of structural complexity was found (Lapinski and Tschapka 2018). In Ecuador the arboreal *Avicularia rufa* was particularly flexible in shelter construction. In microhabitats with a superabundance of hiding possibilities like are offered by palm thatched roofs and by branches full of large tank bromeliads the spiders did not construct significant silken tubes (with the exception of thin molting sacks) rendering them wandering spiders. In microhabitats with scarce hiding possibilities *A. rufa* constructed firm and thick silken tubes and the spiders were found each night in their direct proximity. Thus, high complexity of

vegetation may not only enhance densities of arthropods through providing shelter and food to both predators and their prey (Halaj et al. 2000; Stunz et al. 2002; Teixeira da Souza and Martins 2004), but also affect in some species shelter building behavior and probably site fidelity. The high flexibility may have evolved as a response to the microclimate range from understory to the rainforest canopy, the highly variable microclimate in the canopy (Lapinski and Tschapka 2014) and the ephemeral characteristics of canopy microhabitats with branches or epiphytes breaking off and falling down to the ground. Thus, many arboreal species may face rather instable and hence more variable conditions than inhabitants of the rainforest ground.

7.8 Concluding Remarks

Tarantulas (Theraphosidae) from the New World are widely distributed from northern Utah and California, USA in the north to northern Patagonia, Argentina in the south. Table 7.6 summarizes the information on the tarantula taxa depicted here according to the sequence of the paragraphs in this chapter. However, the ecology of tarantulas has been largely unappreciated. Scarce habitat information comes mainly from taxonomic works and the observations of dedicated amateurs. Tarantulas occupy a variety of different habitats from remote deserts and Caribbean islands, high Andean mountains, dark caves and deep tropical rainforests to plantations, gardens and soccer fields. Some species prefer pristine habitats, other thrive in anthropogenically modified areas, and some are quite flexible and are found in primary rainforest, on houses and road banks in rural areas. The present case study conducted in Costa Rica and Ecuador shows nicely that neotropical rainforests may harbor assemblages of several syntopic tarantula species with two main lifestyles: terrestrial and arboreal. The proportion of arboreal to terrestrial species in the Neotropics may be enhanced by a combination of forests, tree complexity, the presence of water bodies from small to gigantic accompanied by seasonal inundations of huge areas rendering the ground uninhabitable for long periods of time. Within both subguilds habitat segregation may occur at finer scales and include also seasonality patterns. While most terrestrial species live in burrows few take shelter under debris on the forest ground. Some species are found only in the forest interior, others prefer the open ground of small clearings. Arboreal species show high variability in microhabitat choice as long as it is more or less elevated and presents vertical structures: plants of various types and shapes. Buildings are used by several arboreal species as well, especially in the genus *Avicularia*. Here many species seem to be preadapted due to the highly variable conditions they encounter between the understory and the high canopy.

It is evident how underdeveloped our current knowledge and understanding of almost any ecological aspect of even “well-known” and conspicuous tarantula species is. Habitat use and community ecology of tarantulas is even deeper down the

Table 7.6 Summary of ecology of the tarantula taxa depicted in this chapter according to the sequence of the respective paragraphs

Genus/species	Region	Topophilia macro	Topophilia micro
Aphonopelma spp.	USA, Central America	(semi)deserts to temperate high-elevation forests	Silk-lined burrows in the ground
Brachypelma spp. "red-knee"	Mexico, Pacific slope	Dry thorn to high elevation forests, pastures	Silk-lined burrows in the ground
Tliltocatl spp. "red-rump"	Mexico, S & Carribean slope	Dry thorn to high elev. Forests, trop. Evergreen forests,	Silk-lined burrows in the ground
	Central America, Florida (USA)[a]	Other anthropogenically modified habitats[a]	Silk-lined burrows in the ground
Hemirrhagus spp.	Mexico, central to south	Caves, high elevation forests	On floor and walls
Tmesiphantes hypogeus	Brazil, Bahia	Caves	On humid rocky substrates
Lasiodora sp.	Brazil, Bahia	Cave	On cave floor
Avicularia spp.	Trop. South America, Panama	Trop. Rainforest, anthropogenically modified habitats	On vegetation and buildings
Avicularia taunayi	Brazil, NE	Cerrado	Silk tubes in tree holes
Ybyrapora spp.	Brazil, NE	Lowland Atlantic rainforest, primary and secondary	Silk tubes on tree trunks, among leaves,
			In terrestrial bromeliads
Iridopelma spp.	Brazil, NE	Lowland Atlantic rainforest, Restinga, caatinga, cerrado	Silk tubes on leaves, in terrestrial bromeliads,
			Under logs
Pachistopelma spp.	Brazil, NE	Lowland Atlantic rainforest, Restinga, caatinga	Silk tubes in terrestrial bromeliads
Typhochlaena spp.	Brazil, NE	Lowland Atlantic rainforest, Restinga, caatinga, cerrado	Silk tubes with trap door on trees
Dolichothele spp.	Brazil, NE	Lowland Atlantic rainforest, Restinga, caatinga, cerrado	Silk-lined burrows under stones and logs
Agnostopelma spp.	Colombia, Andes	No information available	Under stones
Aguapanela Arvi,	Colombia, Andes	High Andean cloud forest	In rock crevices
Hapalopus sp.*, Ami* sp.	Colombia, Andes	High Andean cloud forest	No information available
Catumiri spp., *Holothele* spp.	Colombia, Andes	No information available	No information available
Cyclosternum gaujoni, C. schmardae	Ecuador, Andes	No information available	No information available
Pamphobeteus augusti, P. vespertinus	Ecuador, Andes	No information available	No information available

(continued)

Table 7.6 (continued)

Genus/species	Region	Topophilia macro	Topophilia micro
Cyriocosmus pribiki, C. rogerioi	Peru, Andes	High Andean cloud forest	No information available
Bistriopelma lamasi, B. matuskai	Peru, Andes	Grass slopes	Under stones and rocks
Hapalotremus spp.	Peru, Andes	Grass slopes	Crevices and burrows under rocks
Hapalotremus spp.	Bolivia, Andes	Yungas	No information available
Hapalotremus martinorum	Argentina, NW, Andes	High Andean cloud forest	No information available
Hapalotremus chasqui	Argentina, NW, Andes	Grass land with tree groves	Under rocks
Euathlus spp.	Chile, Andes	Semi-arid habitats,	No information available
Euathlus diamante	Argentina, NW, Andes	Semi-arid grass and shrubland	No information available
Euathlus sagei	Argentina, NW, Patagonia	Steppe	Crevices and burrows under rocks
Euathlus tenebrarum	Argentina, NW, Patagonia	Humid Andean-Patagonic forests	Crevices and burrows under rocks
Psalmopoeus reduncus	Costa Rica, Sarapiquí region	Tropical rainforest	On trees and other vegetation
Lasiodora icecu	Costa Rica, Sarapiquí region	Tropical rainforest	Burrows in forest ground
Sericoplema silvicola	Costa Rica, Sarapiquí region	Tropical rainforest	Burrows in forest ground
Stichoplastoris obelix	Costa Rica, Sarapiquí region	Tropical rainforest	Burrows in forest ground
Neischnocolus panamanus	Costa Rica, Sarapiquí region	Tropical rainforest	Under wood on forest ground
Neischnocolus yupanquii	Ecuador, Rio Napo	Tropical rainforest	Leaf litter forest ground
Megaphobema velvetosoma	Ecuador, Rio Napo	Tropical rainforest	Burrows in forest ground
Theraphosinae 1	Ecuador, Rio Napo	Tropical rainforest, clearing	Burrows in soil of clearing
Theraphosinae 2	Ecuador, Rio Napo	Tropical rainforest, clearing	On ground
Theraphosinae 3 (Yasuní Tiger Tarant.)	Ecuador, Rio Napo	Tropical rainforest	On leaf understory Maranthaceae
Avicularia hirschii, A.purpurea, A. rufa	Ecuador, Rio Napo	Tropical rainforest	On trees and huts
Pseudoclamoris sp. (cf. *burgessi*)	Ecuador, Rio Napo	Tropical rainforest	On trees

NE north-east, *NW* north-west, *S* south

[a] Refers to *Tliltocatl vagans*

Rabbit Hole—or further up the Tree of Souls—and I hope researchers all over the world start to investigate this overlooked aspect of tarantula biology, daring to enter the higher spheres of the rainforest, to go underground exploring the deeper realms of the earth and observing patiently both the living animals and their surroundings to which they are connected so tightly. Why? Because it is fascinating, important, and fun at the same time!

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