

RESEARCH ARTICLE

Desiccation resistance reflects patterns of microhabitat choice in a Central American assemblage of wandering spiders

Witold Lapinski^{1,*} and Marco Tschapka^{2,3,*}**ABSTRACT**

The lowland rainforest of northeastern Costa Rica harbours an assemblage of large wandering spider species belonging to three habitat subguilds: (1) semi-aquatic, (2) forest ground dwelling and (3) vegetation dwelling. We hypothesized that desiccation resistance should differ among species preferring different microhabitats and the associated microclimate. Desiccation resistance was assessed by: (1) measuring water loss rates of the spiders under relatively dry experimental conditions, and (2) recording desiccation susceptibility, i.e. the reactions of the spiders to a relatively dry environment. High water loss rates and desiccation susceptibility of the semi-aquatic and forest-ground-dwelling subguilds clearly mirrored the relatively humid microclimate of the understory. Significantly lower water loss rates and desiccation susceptibility of the vegetation-dwelling species reflected the highly variable, often dry and hot conditions of the rainforest canopy and forest edge habitats. Vegetation-dwelling wandering spiders are therefore physiologically better adapted to dry conditions than the semi-aquatic and forest-ground-dwelling species. The results illustrate the significance of physiological characteristics for explaining both species-specific habitat use and, in a larger context, niche partitioning within a community.

KEY WORDS: Ecology, Physiology, Rainforest, Ctenidae, Trechaleidae, Canopy

INTRODUCTION

Patterns of sympatry among animals are still not fully understood. Besides interspecific interactions, community patterns may also be influenced by abiotic factors, resulting in specific habitat selection matched to physiological traits (Kneitel and Chase, 2004; Morin, 2011). Because spiders are very diverse and abundant in most habitats, they may serve as model organisms to study some of these traits and their contribution to community organization (Wise, 1993; Barth, 2001; DeVito et al., 2004; Herberstein, 2011). So far, biological aspects of most tropical spiders have been quite poorly studied. Araneomorph wandering spiders are common in the tropics and often form assemblages consisting of seven or more large species (Höfer et al., 1994; Gasnier et al., 2002; Lapinski and Tschapka, 2013). Lapinski and Tschapka (Lapinski and Tschapka, 2013) reported on habitat use within a guild of medium to large species of araneomorph wandering spiders in a Costa Rican lowland rainforest. Species grouped into three habitat subguilds: (1) semi-

aquatic: *Ancylometes bogotensis* (Keyserling 1877) (Ctenidae) and *Trechalea tirimbina* Silva and Lapinski 2012 (Trechaleidae), which were strongly associated with water bodies; (2) forest ground dwellers: *Ctenus curvipes* (Keyserling 1881), *Ctenus sinuatifipes* F.O.P.-Cambridge 1897 and *Ctenus* sp. 3 (Ctenidae), which roam the forest floor and climb occasionally onto the lower vegetation; and (3) vegetation dwellers, which were almost exclusively found on plants: *Cupiennius coccineus* F.O.P.-Cambridge 1901, *Cupiennius getazi* Simon 1891 and *Phoneutria boliviensis* (F.O.P.-Cambridge 1897) (Ctenidae). In the vegetation-dweller subguild, *C. coccineus* was most abundant within the forest and was found up to 11 m above ground on trees, while the latter two species were mainly found on higher vegetation in treeless areas. Distinct differences in their ability to move on smooth surfaces and the corresponding morphological traits matched the ecological preferences of these species (Lapinski and Tschapka, 2013) (W.L. and M.T., unpublished data). This supports the hypothesis that specific traits play key roles in shaping community structure (Kneitel and Chase, 2004).

Previous studies have shown that the microclimate in rainforests is stratified vertically (Kumagai et al., 2001; Madigosky, 2004) and suggested that abiotic factors are among the main parameters determining the vertical distribution of arthropods in tropical forests (Basset et al., 2003; Hurtado Guerrero et al., 2003). Water loss has been measured for different animal taxa, sometimes linking these traits to habitat preferences, but only rarely have actual microclimate data from the habitats of the studied species been presented (e.g. Engelhardt, 1964; Bentley and Schmidt-Nielsen, 1966; Warburg and Ben-Horin, 1978; Hadley et al., 1981; Pulz, 1983; Pulz, 1987; Wygoda, 1984; Buttemer, 1990; Hadley, 1994; Barth, 2001; Young et al., 2005).

The objective of our study was to link physiological traits to the microclimate of the respective habitat, and thus investigate how ecophysiological factors contribute to community organization of spiders. We therefore studied desiccation resistance within a guild of large wandering spider species and the microclimatic conditions in their respective rainforest understory and canopy habitats. We hypothesized that the spider species should differ in their resistance to desiccation and that these physiological adaptations should match the habitat used by the three subguilds. Specifically, we expected an increase in desiccation resistance from semi-aquatic to forest-ground-dwelling to vegetation-dwelling species, corresponding to the microclimate of their preferred microhabitats.

RESULTS**Microclimate**

Temperature was significantly lower at 1 m than at 28 m during the daytime, while during the night it was slightly, though significantly, higher at 1 m than at 28 m. At each given height it was always significantly lower during the night than during the day (Kruskal–Wallis ANOVA, $H_3=5662.4$, $P<0.001$, Dunn's *post hoc* test, $P<0.05$; Fig. 1A). Relative humidity during the day was

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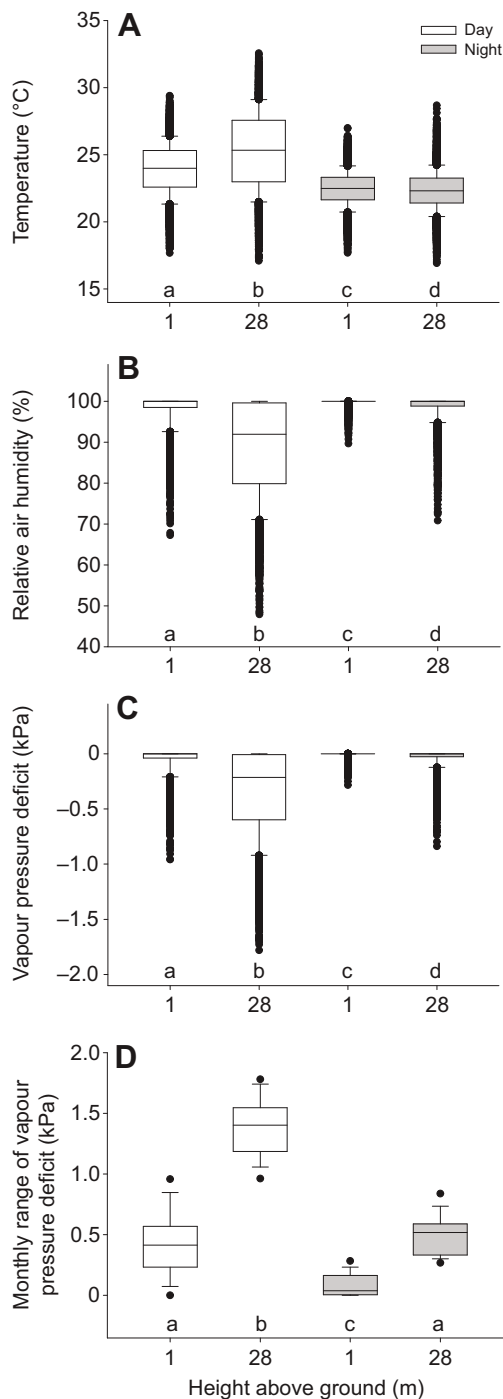


Fig. 1. Comparison of main microclimate parameters between the understory and the canopy of the forest during the day and at night. (A) Temperature; (B) relative air humidity; (C) vapour pressure deficit of the air; (D) monthly range of vapour pressure deficit. Different letters below the plots indicate significant differences between microclimatic data at different heights. Horizontal lines in the boxes represent the median heights. Boxes are from Q_{25} to Q_{75} , error bars are Q_{10} and Q_{90} ; circles are outliers.

significantly higher in the understory than in the canopy, while at night these differences diminished strongly, yet remained significant. Similar to temperature, relative humidity was always significantly higher during the night than during the day (Kruskal–Wallis ANOVA, $H_3=8481.3$, $P \leq 0.001$, Dunn's *post hoc* test, $P < 0.05$; Fig. 1B). During the day, vapour pressure deficit (VPD) showed

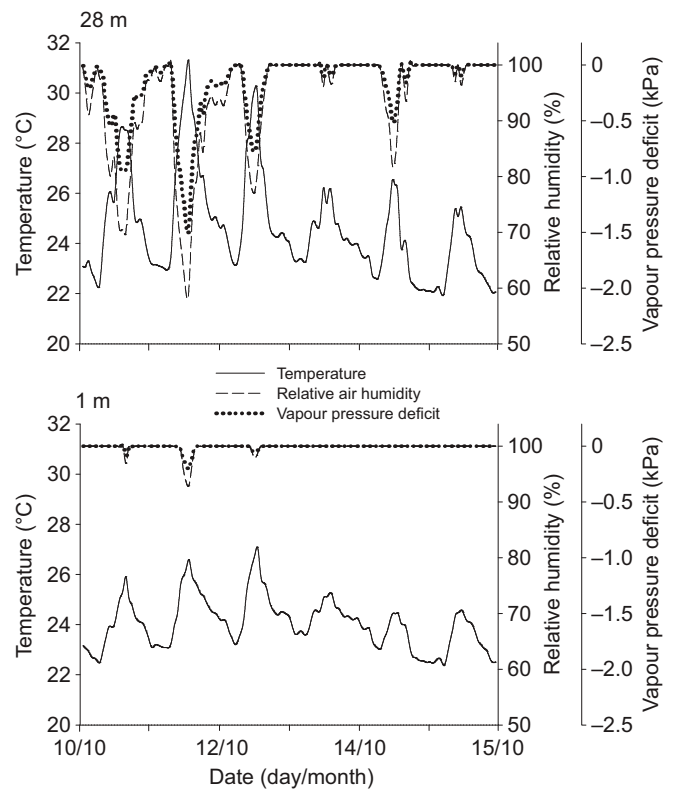


Fig. 2. Examples of the microclimate fluctuations in the canopy and the understory during the period 10–15 October 2010.

significantly lower values in the understory than in the canopy. At night these differences decreased, but were still significant. Within the same height class, VPD was always significantly lower during night than during the day (Kruskal–Wallis ANOVA, $H_3=8477.6$, $P \leq 0.001$, Dunn's *post hoc* test, $P < 0.05$; Fig. 1C). VPD varied significantly more at 28 m than at 1 m both during the day and night. For any given height, VPD fluctuated more during the day than during the night. The monthly variation in VPD recorded within the understory during the day did not differ significantly from values recorded from the canopy at night (Kruskal–Wallis ANOVA, $H_3=53.971$, $P \leq 0.001$, Tukey's *post hoc* test, $P < 0.05$; Fig. 1D). Fluctuations of temperature, relative humidity and VPD were more pronounced in the canopy than in the understory (Fig. 2). In the terrarium of the control group, VPD was 0 kPa; in the test group, VPD ranged between -0.5 and -0.7 kPa. These values were well within the range of VPD in both the understory and the canopy. Only at night did the understory show lower VPD than that presented to the test group (Fig. 1C). In general, the wind at Reserva Biológica Tirimbina during the study period was rather moderate. Actual measurements of wind speed are not available; however, wind in the canopy was usually noticeably stronger than in the understory.

Gravimetry

On average, the spiders of the test group lost between 0.06 and 0.23 g of their body mass over 24 h (Table 1) or 2.9–12.4% of their initial body mass (Table 2). Significant differences in body mass loss between males and females were only found in the control group in *C. curvipes* and *C. sinuatipes* (Fig. 3A, Table 2), and only in the test group in *C. coccineus* (Fig. 3B, Table 2). Thus, gender-specific differences in body mass loss appear to be negligible and for each

Table 1. Summary of body mass loss of the test group after 1 day

Species	Sex	m_0 (g)	s.d. m_0 (g)	m_1 (g)	s.d. m_1 (g)	Δm (g)	s.d. Δm (g)
<i>Trechalea tirimbina</i>	M	1.44	0.22	1.26	0.23	0.18	0.06
	F	1.72	0.32	1.57	0.29	0.16	0.08
<i>Ancylometes bogotensis</i>	M	1.94	0.34	1.77	0.29	0.17	0.09
	F	3.35	1.01	3.12	0.99	0.23	0.06
<i>Ctenus</i> sp. 3	M	1.54	0.35	1.42	0.33	0.12	0.05
	F	2.18	0.31	2.03	0.28	0.15	0.07
<i>Ctenus curvipes</i>	M	0.70	0.08	0.63	0.08	0.07	0.02
	F	0.76	0.15	0.68	0.12	0.08	0.57
<i>Ctenus sinuatipes</i>	M	1.71	0.27	1.58	0.27	0.13	0.05
	F	1.98	0.43	1.80	0.39	0.18	0.06
<i>Cupiennius coccineus</i>	M	1.31	0.23	1.26	0.23	0.06	0.02
	F	2.45	0.57	2.38	0.55	0.07	0.04
<i>Cupiennius getazi</i>	M	1.21	0.32	1.13	0.27	0.08	0.06
	F	1.98	0.78	1.89	0.72	0.08	0.07
<i>Phoneutria boliviensis</i>	M	2.88	0.79	2.75	0.76	0.14	0.08
	F	3.90	1.16	3.74	1.12	0.16	0.10

F, female; M, male; m_0 , average mass of the hydrated spiders; m_1 , average mass of the spiders after 1 day; Δm , body mass loss, i.e. $m_0 - m_1$, after 1 day.

species we pooled the values from both sexes prior to testing for interspecific differences. In almost all species in the control group, body mass loss after 24 h was extremely low, with median values around 1%. One exception in the control group was *C. curvipes*, which showed unusually high body mass loss (median=2.5%); nevertheless, it differed significantly only from *P. boliviensis* (Kruskal–Wallis ANOVA, $H_7=14.695$, $P=0.04$, Dunn's *post hoc* test, $P<0.05$; Fig. 4A). Loss of body mass in the test group kept under drier conditions was significantly higher for all species (Mann–Whitney rank sum tests, all $P\leq 0.001$). Under the drier conditions of the experiment, *C. coccineus* showed the lowest (median=3.1%) and *T. tirimbina* the highest (median=10.5%) body mass loss. *Cupiennius coccineus*, *C. getazi* and *P. boliviensis* showed distinctly, though not always significantly, lower body mass loss than the three *Ctenus* species, *A. bogotensis* and *T. tirimbina* (Kruskal–Wallis ANOVA, $H_7=71.968$, $P\leq 0.001$, Dunn's *post hoc* test $P<0.05$; Fig. 4B). Linear regression analysis showed a

significant negative correlation of the percentage of body mass loss after 1 day and the initial body mass (m_0) of the spiders in females ($R^2=0.0739$, $P=0.015$) but not in males ($R^2=0.0288$, $P=0.145$) when the smallest species *C. curvipes* was included. Because this species is both the smallest species and, as a result of its lifestyle, apparently rather susceptible to desiccation (see above), we assume a double effect (size and microhabitat use) on desiccation resistance. Therefore, we performed a second regression analysis without that species and we found no significant correlation between the percentage of body mass loss after 1 day and m_0 of the spiders in both sexes (females: $R^2=0.033$, $P=0.135$; males: $R^2=0.006$, $P=0.538$; Fig. 5).

Susceptibility to desiccation

In the control group, all individuals survived without showing any desiccation effects. In the test group, in contrast, mainly individuals of *T. tirimbina*, *A. bogotensis* and the three *Ctenus* spp. showed

Table 2. Average percentage of body mass loss in the control and the test groups after 1 day and the respective test statistics

	Males (%)	Variability (%)	Females (%)	Variability (%)	t or T	d.f.	P
Control group							
<i>Trechalea tirimbina</i>	0.9	0.5	1.3	1.1	-0.7	11	0.49*
<i>Ancylometes bogotensis</i>	0.9	0.8	1.7	1.3	-1.48	15	0.17*
<i>Ctenus</i> sp. 3	0.6	0.4; 0.9	1.8	0.3; 3.2	94.0	–	0.43#
<i>Ctenus curvipes</i>	1.3	0.3; 2.0	5.6	2.7; 8.0	50.0	–	0.02#
<i>Ctenus sinuatipes</i>	0.6	0.03; 1.1	2.1	1.1; 3.5	45.0	–	0.02#
<i>Cupiennius coccineus</i>	1.5	0.7	1.5	1.1	-0.05	16	0.96*
<i>Cupiennius getazi</i>	1.3	0.9	1.8	1.1	-1.21	16	0.24*
<i>Phoneutria boliviensis</i>	0.5	0.4	1.1	0.6	-1.97	10	0.08*
	Males (%)	Variability (%)	Females (%)	Variability (%)	t	d.f.	P
Test group							
<i>Trechalea tirimbina</i>	12.4	4.7	9.0	3.9	1.67	15	0.12*
<i>Ancylometes bogotensis</i>	8.7	3.4	7.2	2.5	1.13	17	0.27*
<i>Ctenus</i> sp. 3	8.0	2.6	6.5	2.5	1.25	18	0.23*
<i>Ctenus curvipes</i>	9.4	8.1; 10.4	9.1	5.2; 10.8	108.0	–	0.85#
<i>Ctenus sinuatipes</i>	7.9	2.7	9.2	2.3	-1.19	18	0.25*
<i>Cupiennius coccineus</i>	4.4	1.3	2.9	1.1	2.87	18	0.01*
<i>Cupiennius getazi</i>	6.1	3.2	4.0	2.1	1.68	18	0.11*
<i>Phoneutria boliviensis</i>	4.7	2.3	4.1	1.8	0.63	16	0.54*

* t -test.

#Mann–Whitney rank sum test.

Variability is either s.d. or Q_{25} and Q_{75} , depending on the test.

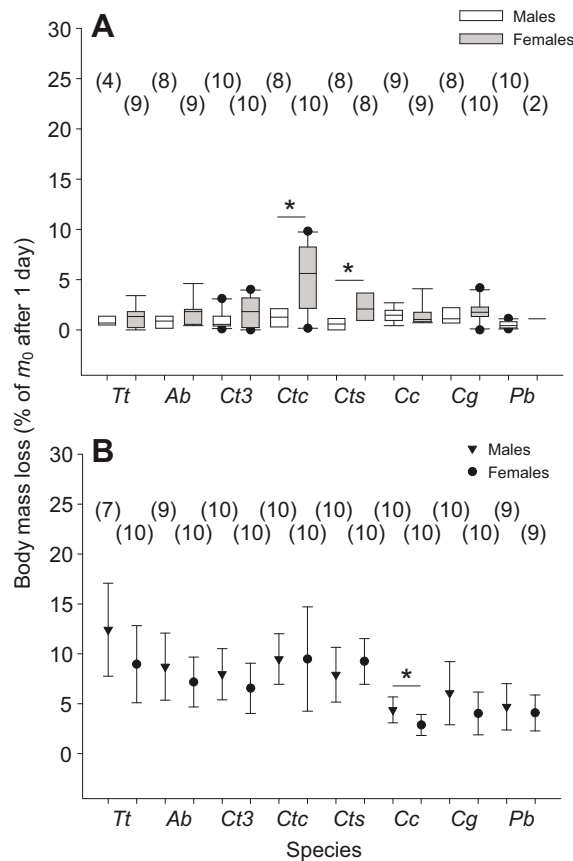


Fig. 3. Intraspecific comparisons of body mass loss after 1 day between sexes. (A) Control group. Horizontal lines in the boxes represent the median, boxes are from Q_{25} to Q_{75} , error bars are Q_{10} and Q_{90} ; circles are outliers. (B) Spiders kept under drier conditions. Numbers in parentheses above the plots give the number of spiders measured; * indicates a significant difference between males and females. Species abbreviations: *Tt*, *Trechalea tirimbina*; *Ab*, *Ancylometes bogotensis*; *Ct3*, *Ctenus* sp. 3; *Ctc*, *Ctenus curvipes*; *Cts*, *Ctenus sinuatipes*; *Cc*, *Cupiennius coccineus*; *Cg*, *Cupiennius getazi*; *Pb*, *Phoneutria boliviensis*.

various desiccation effects, e.g. bent legs that resulted in a more or less impeded locomotion (Fig. 6).

Day shelters of the species

All species were predominantly active at night. Whenever possible we made additional observations on day shelters of the species. In general, *Ancylometes bogotensis* used cavities or burrows in the ground, hollow logs or hollowed-out banks. On cloudy and cool days this species was sometimes found out of its shelter, always on wet ground close to water bodies. *Trechalea tirimbina* spent the day usually in the darker parts of logs above creeks or in hollowed-out banks; the substrate was usually wet. The three *Ctenus* spp. mainly sheltered in burrows or under wood on the forest ground, and sometimes among leaf litter. *Cupiennius coccineus* was mainly found within rolled dead leaves or among dead and live leaves at greater heights, and sometimes freely on tree trunks, only shaded by vine leaves or resting on palm leaves. On two occasions this species was observed in its day shelter in the canopy: under dry moss at 31 m above ground on the trunk of a *Ceiba pentandra*, and in a crotch of a large branch making a shallow and broad depression in the trunk of a *Luehea seemanii*, approximately 24 m above ground. *Cupiennius getazi* occurred during the day among or freely on leaves in a temporary swamp. We did not find any day shelters of *P. boliviensis*.

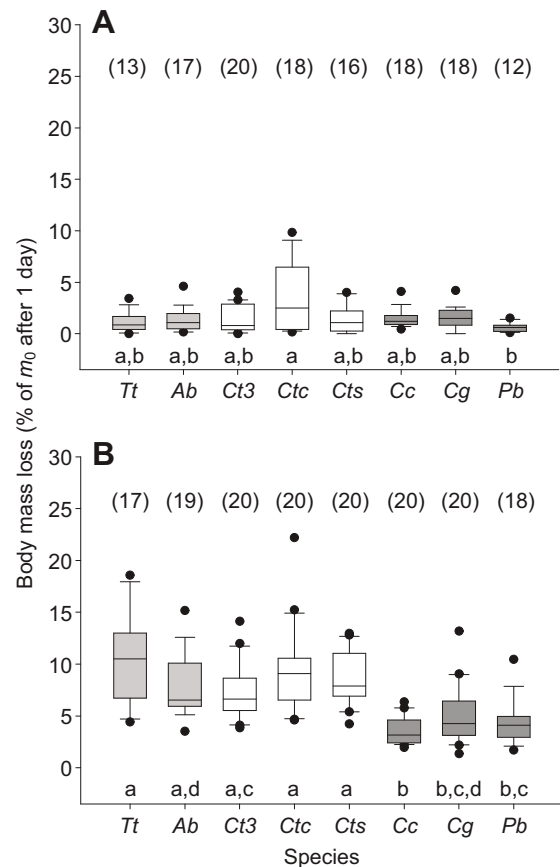


Fig. 4. Body mass loss after 1 day in the studied spiders. (A) Control group; (B) spiders kept under drier conditions. Numbers in parentheses above box plots give the number of spiders measured; different letters below the box plots indicate significant differences among species. The fill colours of the box plots indicate the subguilds: grey, semi-aquatic; white, forest ground dwelling; dark grey, vegetation dwelling. For species abbreviations, see legend to Fig. 3. Horizontal lines in the boxes represent the median, boxes are from Q_{25} to Q_{75} , error bars are Q_{10} and Q_{90} ; circles are outliers.

DISCUSSION

Our study provides a comparison of the specific susceptibility to water loss within an assemblage of large wandering spiders consisting of seven ctenid and one trechaleid species, and links these physiological traits to the microclimate of their respective forest understory and canopy habitats (Lapinski and Tschapka, 2013). Our measurements show a more variable and more extreme microclimate in the canopy than in the understory both during the day and at night, corroborating results from other studies (Kumagai et al., 2001; Madigosky, 2004).

We took care to present rather realistic climatic situations for the spiders, and matched microclimate conditions during the experiments closely to the range measured in the field. The VPD presented to the test group exceeded slightly the values recorded at night in the understory. The low body mass decrease of the control group shows that our setup did not generate general stress for the spiders, which otherwise could have affected the measurements and caused much higher mortality (DeVito et al., 2004). In contrast to the very low losses in body mass in the control group, there were significantly higher decreases under the drier conditions of the test group, which therefore can be mainly attributed to water loss. The unusually high body mass decrease of female *C. curvipes* in the control group might also be the result from higher activity; however, we did not notice any unusual behaviour in that species.

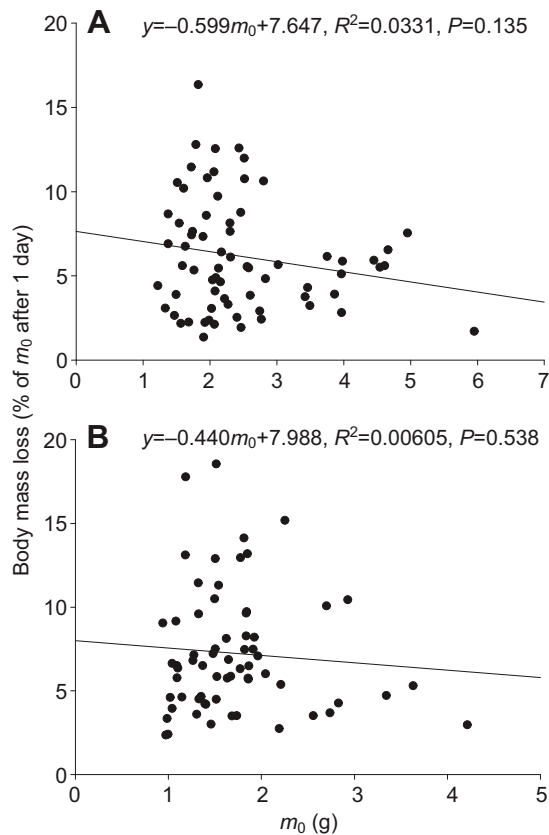


Fig. 5. Results of linear regression analyses of the body mass loss after 1 day versus initial body mass (m_0) of the spiders in the test group. (A) Females; (B) males. *Ctenus curvipes*, the smallest species, was excluded from the analysis.

Nevertheless, even in this species body-mass loss remained significantly lower in the control group than in the test group.

Our data indicate significant differences in tolerance to relatively dry conditions among the species and the subguilds *sensu* Lapinski and Tschapka (Lapinski and Tschapka, 2013). The studied species showed no differences in general patterns of activity (Lapinski and Tschapka, 2013). Because there were no consistent intraspecific differences in desiccation resistance between sexes and no significant correlations between desiccation resistance and initial body mass of most species, we suggest that the observed differences in desiccation resistance between species are primarily related to or determine their habitat use. There were no significant differences between the semi-aquatic and forest-ground-dwelling species, but both subguilds showed a distinctly lower desiccation resistance than the vegetation dwellers. Although not all species comparisons showed significant differences, our hypothesis of distinct dissimilarities in desiccation resistance, corresponding to the habitat subguilds, was partially confirmed.

The underlying factors actually causing these guild-specific differences may be rather diverse. Small animals such as arthropods generally have a high surface area to body mass ratio and thus experience fast heat gain and high water loss rates (Hadley, 1990). The surface area increases with the length of appendages (Eisenbeis and Wichard, 2003). There were no great intraspecific differences in the ratio of leg span to body mass (LS/ m) in either sex, with females of *A. bogotensis* having a lower LS/ m ratio than females of *T. tirimbina*, both semi-aquatic species. The LS/ m values of the

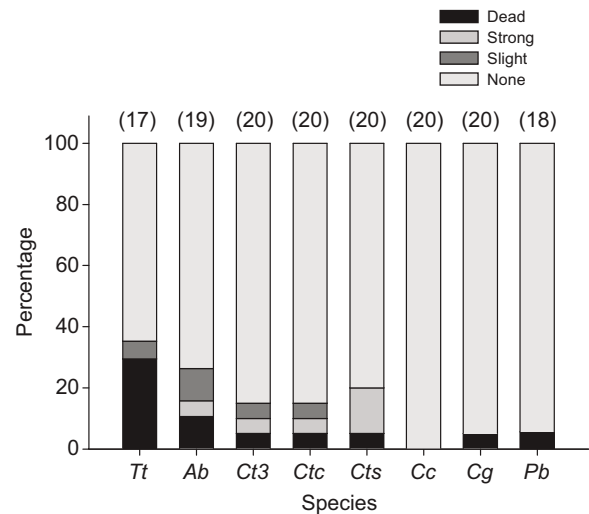


Fig. 6. Percentage of wandering spiders showing desiccation effects on body condition under drier conditions during the experiment. None, no effect visible; slight, slightly bent legs; strong, strongly bent legs and impeded locomotion. Numbers in parentheses above the columns give the number of spiders measured; for species abbreviations, see legend to Fig. 3.

ground and vegetation dwellers were intermediate. Among males, only the LS/ m of *C. curvipes* was significantly higher than that of *P. boliviensis*, with the other species being in between (W.L. and M.T., unpublished data). These findings indicate that the differences in surface area to mass ratio play a rather negligible role in the present context. Moreover, our smallest species, *C. curvipes*, did not show the highest body mass losses. Instead, those occurred in the semi-aquatic *T. tirimbina*, probably because of its very long legs (W.L. and M.T., unpublished data) increasing the evaporative surface area (Eisenbeis and Wichard, 2003) and/or a different composition of cuticular lipids (Pulz, 1987; Hadley, 1990) that might be typical for a genus that is largely associated with water and that – as a member of the Trechaleidae family – is phylogenetically most distant from the other species in this study, which all belonged into the Ctenidae family. The arboreal *C. coccineus* showed the highest desiccation resistance of all studied species, followed by *P. boliviensis* and *C. getazi*. Barth (Barth, 2001) reports that lethal water loss was approximately 13–21% in *C. coccineus* and 12–15% in *C. getazi*. These results imply a higher desiccation resistance of *C. coccineus* than of *C. getazi* and are in accordance with our data.

The specific differences in water loss rates were reflected by the effects of desiccation on the body condition of the spiders. In contrast to the vegetation dwellers, both semi-aquatic species and forest-ground dwellers showed very strong signs of desiccation stress under the drier experimental conditions, manifested in strongly bent legs and slow movements, and occasionally even in death. Similar results were found for *Pirata sedentarius* (Lycosidae), a species that occurs most frequently close to creeks, and it also exhibited the lowest desiccation resistance (DeVito et al., 2004).

Physiological tolerance of the studied species thus clearly reflected the microclimate conditions of the respective microhabitat. This confirmed partly our hypothesis and corroborates previous findings of lower water loss rates and higher desiccation resistance in animals from drier habitats, including the highly variable forest canopy (e.g. Engelhardt, 1964; Warburg and Ben-Horin, 1978; Eynan and Dmi'el, 1993; DeVito et al., 2004; Schilman et al., 2005; Young et al., 2005). Xeric insects show lower water loss rates and have a greater proportion of respiratory transpiration in total water

loss than mesic species (Addo-Bediako et al., 2001). With the exception of the trechaleid *T. tirimbina*, all species studied are from the Ctenidae family, so no distinct phylogenetically based differences influencing desiccation resistance, e.g. in respiratory organs or cuticula composition, can be expected; however, should these exist, they are probably adaptive and reflect the actual habitat use. The actual physiological mechanisms underlying the observed differences in desiccation resistance remain to be investigated.

Our results suggest that semi-aquatic and forest-ground-dwelling spider species of humid tropics face a similar and, over evolutionary time, relatively stable microclimate that has exerted no strong selection towards physiological adaptations for dry conditions. Nevertheless, behavioural adaptations, such as taking shelter during the hottest time of the day, still exist (Foelix, 1992; Wise, 1993). The semi-aquatic species avoided desiccation by spending the day in shelters or on wet substrates close to the forest floor and/or water. Even at night the canopy presented a higher and more variable VPD than during the day. Because of these microclimatic differences of the forest and the species' low desiccation resistance, these species are restricted to the understory. In contrast, vegetation-dwelling, especially arboreal, species are likely to face a much more variable microclimate. *Cupiennius coccineus* and *C. getazi* were observed frequently to spend the day outside their shelters, well camouflaged yet exposed to the respective microclimatic conditions. Barth et al. (Barth et al., 1988) showed that some shelters of *Cupiennius* spp. may present much lower evaporation than the surrounding air during both day and night, and that even within the shelters evaporation may be much higher during the day than during the night. *Cupiennius getazi* can sometimes even be found during the day outside shelters, freely exposed on vegetation (Schuster et al., 1994; present study). Thus vegetation-dwelling species may experience more pronounced microclimatic changes over the course of a day than the forest-ground-dwelling and semi-aquatic species. Here, evolution seems to have selected for more effective physiological adaptations against desiccation (Hood and Tschinkel, 1990). Additionally, arboreal species might track more adequate climatic conditions by vertical movements along the vertical temperature and relative humidity variation gradients, as found in the vegetation-dwelling *Oxyopes salticus* (Oxyopidae) (Vollmer and MacMahon, 1974). In contrast, similar physiological tolerances might also be more related to close phylogenetic relationships than to adaptations to a specific habitat (Addo-Bediako et al., 2001; Chown, 2002). However, this does not seem very likely in our study when considering the current phylogeny of the Ctenoidea (Silva Dávila, 2003). Desiccation resistance was low in two not closely related ctenid genera (*Ancylometes* and *Ctenus*) and one trechaleid genus, while it was high in two other, not closely related ctenid genera (*Cupiennius* and *Phoneutria*). Studies on other animal taxa suggest that abiotic habitat characteristics and habitat preferences frequently explain physiological differences better than phylogeny (e.g. Wygoda, 1984; Lahav and Dmi'el, 1996; Young et al., 2005). Our results corroborate that microhabitat choice within spider communities is affected by species-specific adaptations to different microclimate parameters of the habitats (Wise, 1993; DeVito et al., 2004; Entling et al., 2007), thus confirming the general notion that abiotic factors may profoundly influence mechanisms of species coexistence (Kneitel and Chase, 2004; Morin, 2011).

In conclusion, our study showed distinct interactions between the physiological traits of the wandering spider species and the microclimatic conditions of the respective habitat used. The degree of tolerance to certain climatic factors may constrain or enable species to live in a particular habitat. At a broader scale, community

organization in a given region may also be driven by these interactions. Nevertheless, coexistence patterns among species with similar climatic tolerances that can access a particular habitat may also be affected at a finer scale by biotic interactions.

MATERIALS AND METHODS

Study area

The study was conducted from May 2010 to February 2012 at the Reserva Biológica Tirimbina (10°24'N, 84°07'W, 180–220 m a.s.l.), Costa Rica, Heredia Province. The Reserva Biológica Tirimbina includes areas belonging to two life zones: very humid tropical pre-montane forest and transitions to very humid tropical forest (Holdridge, 1967). Eighty-five percent of the reserve's forest is classified as primary forest. For a more detailed description, see Lapinski and Tschapka (Lapinski and Tschapka, 2013).

Microclimate

From 1 October 2010 until 27 February 2012, data loggers (Hobo[®] Pro v2. temp/RH, Onset Computer Corporation, Cape Cod, MA, USA) were installed on three trees at 1 and 28 m above the ground using the single rope technique. They recorded temperature (°C) and relative air humidity (%) every hour. We obtained 148.032-hourly temperature and relative humidity values from 514 days at both heights of those three trees. To record the microclimate likely to be experienced by the spiders in their actual microhabitats instead of the general local climate, the loggers were attached closely to the bark surface (ca. 5 cm). To avoid direct sunlight, the loggers were located on the northern side of the trunks; for protection against rain they were put into horizontally attached 25 cm long white plastic tubes with a diameter of 15 cm. To allow air circulation, a large portion of the plastic on the lower side of the tubes was cut away. Because vapour pressure deficit (VPD) is the force that drives evaporation (Anderson, 1936; Gates, 1980), it was calculated from the recorded temperature and relative humidity data using the formula of Allen et al. (Allen et al., 2005).

Desiccation resistance

Spiders were located during the night with headlamps and brought to the laboratory. Because the spiders occurred at quite low densities, we used individuals of the studied species found throughout the study period. We quantified rates of body mass loss under defined conditions as a direct indicator of specific desiccation resistance. Body mass loss was assessed using gravimetry under field-laboratory conditions. Each spider was maintained in a clear plastic box (10×10×6 cm) with air holes. Because body condition, e.g. the state of hydration or energy reserves, determines actual water loss rates (Pulz, 1987; DeVito et al., 2004), the spiders were supplied with water *ad libitum* during the first night, offering wet tissue paper as substrate, and if malnourished (i.e. spiders with very small opisthosoma) were fed to reach normal mass and hydration conditions. After the first night, the spiders were divided randomly into a test group and a control group. Spiders of the test group were transferred individually into clean, dry plastic boxes that were stacked into a glass terrarium (80×40×40 cm) with 75–80% relative humidity, or a VPD between –0.5 and –0.7 kPa, i.e. a relatively dry rainforest condition (Kumagai et al., 2001; Madigosky, 2004). To achieve these values, the bottom of the terrarium was covered by an oversaturated NaCl solution (ca. 3 cm high) (Engelhardt, 1964). The control group was maintained in a terrarium with water instead of the NaCl solution, and the plastic boxes were lined with moist tissue paper and sprayed with water to ensure moist conditions and a constant water supply for the spiders. Thus VPD in the control group was 0 kPa, which means that any loss of body mass in the control group should be due to factors other than water loss (e.g. defecation). Each terrarium was covered by a glass plate in order to maintain the desired humidity conditions. The two terrariums were placed side by side to ensure the same temperature regime for both groups. Day temperatures in our field laboratory, and thus in the terrariums, varied between 23 and 26°C. At night, 50 W light bulbs under the terrariums were used to maintain this range of microclimate conditions. Each individual of either group was weighed during the first afternoon after collection ($m_0=100\%$ body mass) and again 24 h later on the following afternoon, using a precision balance (VIC-303, accuracy 0.001 g, Acculab Sartorius Group, Goettingen, Germany). In both groups animals lost mass

through using their body reserves, but animals of the test group were additionally not able to replace evaporated water by drinking. Some individuals showed considerable effects of desiccation on locomotion (i.e. impeded movements and more or less bent legs). Desiccated scorpions show similarly reduced extension ability of their limbs (Sensenig and Shultz, 2004). Preliminary experiments conducted at a higher temperature of 30°C showed that animals with the described desiccation effects would die if not removed from the experiment and supplied with water. In case an individual died near the end of the experimental period, the data from the freshly deceased individual were included in the analysis. In addition to the data on body mass loss, observations on the degree of desiccation effects on body condition (slight/strong/dead) were recorded. To avoid repetitive measuring of individuals, all animals were marked after the experiment with non-water-soluble correction fluid (TiPex™) before releasing them at the collection site.

Statistical analyses

Microclimate data from all trees were pooled and compared for differences between heights (i.e. 1 versus 28 m) and between day and night. To assess the variability of VPD, we calculated the monthly range (Köhler et al., 1996): $R = VPD_{\max} - VPD_{\min}$, where VPD_{\max} is the maximum and VPD_{\min} is the minimum value of VPD. Differences in microclimate and interspecific differences in body mass loss within both treatment groups were compared with a Kruskal–Wallis one-way ANOVA on ranks with a *post hoc* Dunn's test for unequal sample sizes. Intraspecific differences in body mass loss between the two treatment groups were tested with a *t*-test (for normally distributed data) or Mann–Whitney rank sum test (for non-normally distributed data). All statistical analyses were conducted using SigmaStat (v3.5) on untransformed data.

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Competing interests

The authors declare no competing financial interests.

Author contributions

All authors contributed to the study design and to the writing of the paper. W.L. conducted the field and laboratory work and data analysis.

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