Revista Ibérica de Aracnología, nº **41** (31/12/2022): 9–14.
Grupo Ibérico de Aracnología (S.E.A.). ISSN: 1576 - 9518.

SPATIOTEMPORAL SEGREGATION OF THE SYMPATRIC SPECIES *CUPIENNIUS GETAZI* AND *C. COCCINEUS* (ARANEAE: TRECHALEIDAE) IN PACUARE NATURE RESERVE, COSTA RICA

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Abstract: The coexistence of species with similar ecological requirements is explained by resource partitioning. Spiders are a good model to test hypotheses about niche segregation between co-occurring species. Here, we analysed the spatiotemporal segregation of the sympatric species *Cupiennius getazi* and *C. coccineus* in a tropical forest of Costa Rica. Significant differences were found in the habitat of each species, with *C. getazi* mainly appearing in the reserve track and *C. coccineus* in the swamp zones. No differences between species were found in the daily activity patterns. Juveniles appeared at lower height in the vegetation than adults/subadults, but no differences between species were found in the height at which they appeared in the vegetation. The orange morphotype of *C. getazi* was more frequent than the grey morphotype. Cannibalism is reported in *C. coccineus*. Differential habitat use indicates a spatial segregation between these species. The intraspecific differences regarding the vertical distribution could contribute to reducing cannibalism in these spiders.
Key words: Araneae, Trechaleidae, wandering spiders, cannibalism, activity patterns, habitat use, Costa Rica.

Segregación espaciotemporal de las especies simpátricas *Cupiennius getazi y C. coccineus* (Araneae: Trechaleidae) en la Reserva Natural de Pacuare, Costa Rica
Resumen: La coexistencia de especies con necesidades ecológicas similares se explica por reparto de recursos. Las arañas son un buen modelo para contrastar hipótesis sobre segregación de nichos entre especies coocurrentes. Aquí analizamos la segregación espaciotemporal de las especies simpátricas *Cupiennius getazi* y *C. coccineus* en un bosque tropical de Costa Rica. Se encontraron diferencias significativas en el hábitat de cada especie, apareciendo *C. getazi* principalmente en el sendero de la reserva y *C. coccineus* en las zonas pantanosas. No se encontraron diferencias entre especies respecto a los patrones de actividad diarios. Los juveniles aparecieron a alturas más bajas de vegetacion que los adultos/subadultos, pero no se encontraron diferencias entre especies respecto a la altura a la que aparecían en la vegetación. El morfotipo naranja de *C. getazi* fue mas frecuente que el morfotipo gris. Se reporta canibalismo en *C. coccineus*. Las diferencias en el uso del hábitat indican segregación espacial entre estas especies. Las diferencias intraespecíficas obtenidas respecto a la distribución vertical podrían contribuir a reducir el canibalismo en estas arañas.
Palabras clave: Araneae, Trechaleidae, arañas errantes, canibalismo, patrones de actividad, uso de hábitat, Costa Rica.

Introduction

Understanding the mechanisms that maintain high levels of biodiversity in ecosystems is one of the main goals of ecology (Hutchinson, 1959). The strong competitive interactions between sympatric species with similar ecological requirements will lead to the extinction of the less competitive species (Hardin, 1960). Consequently, the coexistence of this kind of species can not be possible without niche resource partitioning, which reduces interspecific competition (Chesson, 2000). Resource partitioning has been reported for many taxa of vertebrates and invertebrates (Di Bitetti et al., 2010; Boyer & Rivault, 2006).

Among invertebrates, spiders have been considered a suitable model to study the segregation of similar co-occurring species due to their high abundance, efficiency of sampling, and diversity of lifestyles (Uetz, 1977; Wise, 1995; Michalko & Pekar, 2015). In spiders, resource partitioning has been typically explained by: 1) variation in prey spectrum, due to different hunting strategies or body size (Olive, 1980); 2) activity time, as a consequence of different phenologies or circadian cycles (Ward & Lubin, 1992) and 3) spatial segregation, as a result of different microhabitat or vertical distribution preferences (Cutler & Jennings, 1992). Niche partitioning studies in spiders have been conducted in a wide range of groups, including web-builders (Aiken & Coyle, 2000; Henaut et al., 2001; Novak et al., 2010;) and wandering spiders (Gasnier & Höfer, 2001; Carrel, 2003; Nieto-Castañeda & Jiménez-Jiménez, 2009).

The nocturnal wandering spiders of the neotropical genus *Cupiennius* Simon, 1891 from the family Trechaleidae are a good model system to study niche partitioning.

Cupiennius getazi Simon, 1891 and *C. coccineus* F.O. Pickard-Cambridge, 1901 inhabit sympatrically the Caribbean lowlands of Costa Rica and Panama (Barth et al. 1988). Both species hunt on a similar size group of prey and form a vegetation dwellers subguild (Lapinski & Tschapka, 2013). An ecological guild is defined by a group of species that use the same resources in the same way (Root 1967) and may therefore compete. In spiders, the competition for the same resources influences population structure, microhabitat use and the proportion of adults and juveniles (Riechert & Candy, 1983). The daily locomotor activity patterns of *C. getazi* and *C. coccineus* were measured "ex situ" by Schmitt et al. (1990), suggesting time segregation as a result of differences in their circadian cycles. However, these results from laboratory experiments, where the conditions are not natural, might not be transferable to a field situation. Then, Lapinski & Tschapka (2013) did not detect species-specific hunting times in the field, however the study revealed habitat segregation in

these species, previously documented in Schuster et al. (1994). Later, Lapinski & Tschapka (2018) reported vertical distribution segregation between the instars of *Cupiennius*, which would reduce intraspecific competition and cannibalism.

In this study, we measured in the field for the first time the daily activity patterns of *C. getazi* and *C. coccineus*. The present study aimed to: 1) analyze the spatiotemporal segregation by comparing the daily activity patterns of the species in two habitats (track and swamp); 2) determine if there are inter and intraspecific preferences by comparing the heights on the vegetation at which the spiders were located (vertical distribution); and 3) provide new insights of natural history of the species.

Materials and Methods

Both studied species reach large size and are easily recognisable: *Cupiennius coccineus* presents an inconspicuous gray-brown coloration with dark stripes in legs and dark hearted shaped marks in the opisthosoma (Fig. 1A-B); However, *C. getazi* presents two conspicuous morphotypes, with either grayish or orange basic coloration, and a dorsal dark stripe V-shaped distally in the opisthosoma (Barth & Schmitt, 1991; Barth & Cordes, 1998; Barth, 2002) (Fig. 1C-D). *Cupiennius* spiders seems to be active all year long, with no clear seasonal fluctuations (Lapinski & Tschapka, 2018)

The study was carried out at Pacuare Nature Reserve (Costa Rica), a small private reserve between Tortuguero National Park and Puerto Limón city. This area comprises 800 ha of secondary tropical forest and swamps surrounded by the canals of Tortuguero and the sea (Fig. 2A). The maximum altitude of the reserve does not surpass 1 m above the sea level and its limits are 10º13'50"N / 83º16'7"W at north and 10º12'50"N / 83º13'22"W at south (Abellá et al., 2008).

Sampling consisted in visual search, carried out for 8 nights, from 11 to 19 May of 2019. The weather conditions of the sampling nights were very similar, with open sky. Within the reserve, two different areas were selected: 1) the main track that connects the north and south stations, near the beach (Fig. 2B) and 2) the swamp zones, further inland into the forest (Fig. 2C). Both areas were sampled with headlights from sunset (18:30) to sunrise (05:00) in order to determine the spatiotemporal segregation of the species. The following time intervals were used once per area: 18:30-21:00, 21:00-00:00, 00:00-02:30, 02:30-05:00. We took data of all active individuals observed of both species, writing down the time and height where they were found. As Lapinski & Tschapka (2018), we distinguish between two instar stages: adult/subadult spiders and juvenile spiders (0.5≥ body length of adults/subadults). The smallest juveniles (≤3 mm body length) were excluded because of the difficulty of identification in the field. With the aim of disentangling the intra and interspecific preferences, the height was classified into five categories depending on the vegetation structure: 1) "very low" (0-50 cm), 2) "low" (50-100 cm), 3) "medium" (100-150 cm), 4) "high" (150-200 cm) and 5) "very high" (>200 cm). In addition, for *C. getazi* individuals, we differentiate among the orange and gray morphotypes to establish the proportion of colors. Total data collected along the eight days of sampling is shown in Supplementary Table SS. 1.

We used a Chi-square test to test the intra and interspecific differences regarding the height and the interspecific differences of the area where the spiders were found. The differences in the activity patterns between the species were tested with type II ANOVA. The variables were transformed with a logit function; and normality and homoscedasticity were tested with the Shapiro-Wilk (p=0.620) and ncvTest (score test for Non-Constant error Variance) (p=0.822), respectively. Analyses were conducted in R software (R Core Team, 2020) using the packages "lattice" (Sarkar and Deepayan, 2008) and "car" (Fox and Weisberg, 2019).

Results

We observed a total of 215 spiders, 39 individuals of *Cupiennius getazi* and 176 of *C. coccineus*. The Chi-square test indicated significant differences (df=1, p<0.001) in the area where the spiders were found. Most *C. getazi* individuals were seen in the track area (track=32, swamps=7) whereas *C. coccineus* was more likely to be seen in the swamp zones (track=9, swamps=167).

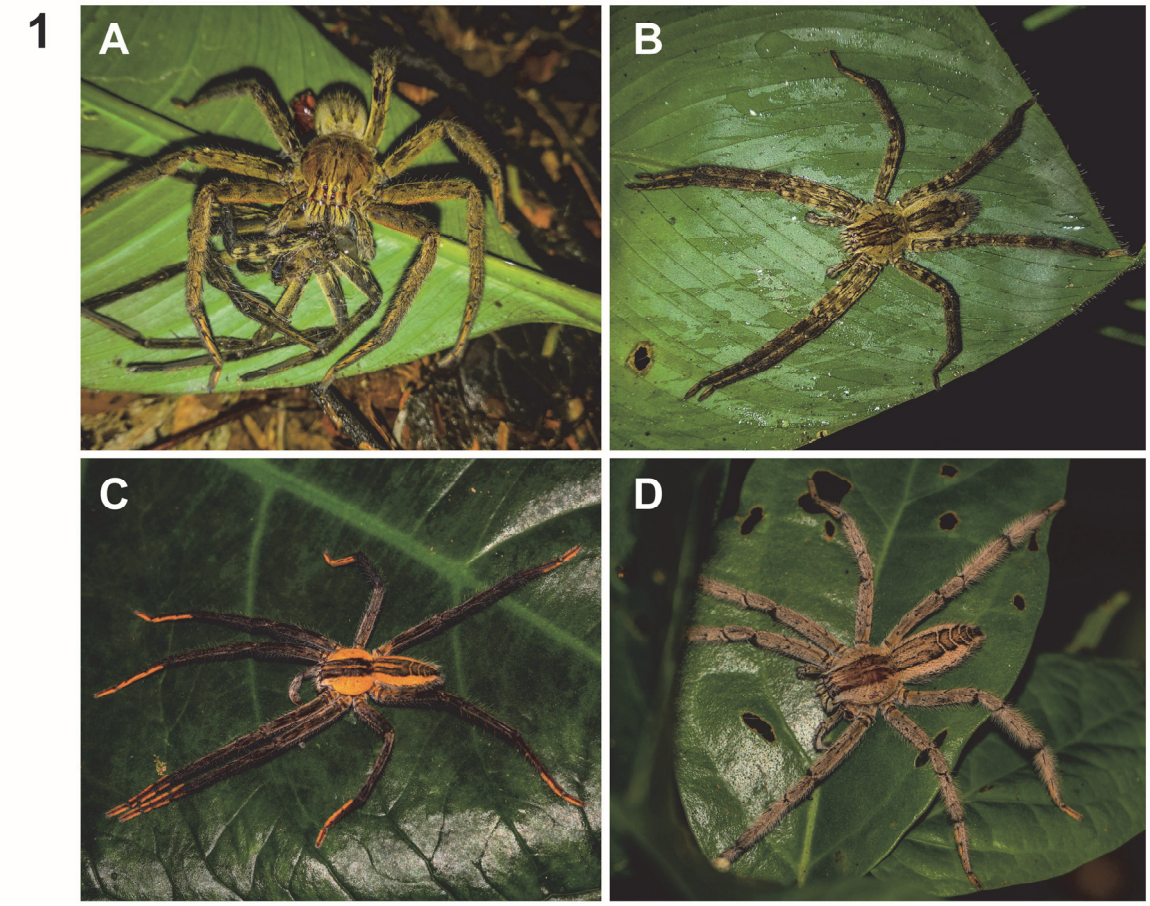
There were non-significant differences between species in the daily activity patterns (Anova type II test, F=0.8, df=1, p=0.565). Both species followed a similar pattern with four activity peaks: two centrals, one in the beginning of the night and other in the fall, separated each one by approximately three hours (Fig. 3). The maximum activity peak of *C. getazi* occurs at the beginning of the night (18:30-19:30, n=7), followed by the two centrals (22:30-23:30, n=6 and 01:30-02:30, n=5) and the fall one (03:30-04:30, n=5) respectively. In *C. coccineus*, the maximum activity peak occurs in the first central peak (21:30-22:30, n=23), followed by the fall (02:30-03:30, n=21), the beginning (18:30-19:30, n=20) and finally, the second central (00:30-01:30, n=10).

There were no interspecific differences (df=4, p =0,25) in the vertical distribution of the species. Most of the individuals were found at "low", followed by "very low" vegetation (Fig. 4A). The vertical distribution significantly differed between instars (Chi-square test, df=4, p< 0.001). Most juveniles were found at "very low" and "low" height while adult presence peaked at "low" height and were present at "very high" vegetation height (Fig. 4B).

87 % (n=34) of the observed *C. getazi* individuals presented the orange morphotype, whereas the gray one is represented by the 13% (n=4).

Discussion

Cupiennius coccineus was four times more abundant than *C. getazi*, as previous studies have already reported *C. coccineus* as the most abundant species sampled (Schuster et al., 1994; Lapinski & Tschapka, 2013, 2018). The coexistence of these spiders is predicted by niche theory, which suggests that it is based on species-specific use of resources (Putman, 1994). These species are clearly segregated spatially, predominantly, *C. coccineus* was found more frequently in the swamp zones whereas *C. getazi* was found in the track. As some authors have addressed, this could be a consequence to their ecological requirements: "*C. coccineus* prefers forest sites, while *C. getazi* is a habitat generalist that may prefer treeless areas" (Schuster et al., 1994; Lapinski & Tschapka, 2013). Our observations fit well with Lapinski & Tschapka (2013) work at Tirimbina Biological Reserve, where they found *C. getazi* mainly in a treeless temporary swamp and *C. coccineus* only in the reserve forest. Additionally, not a single individual of



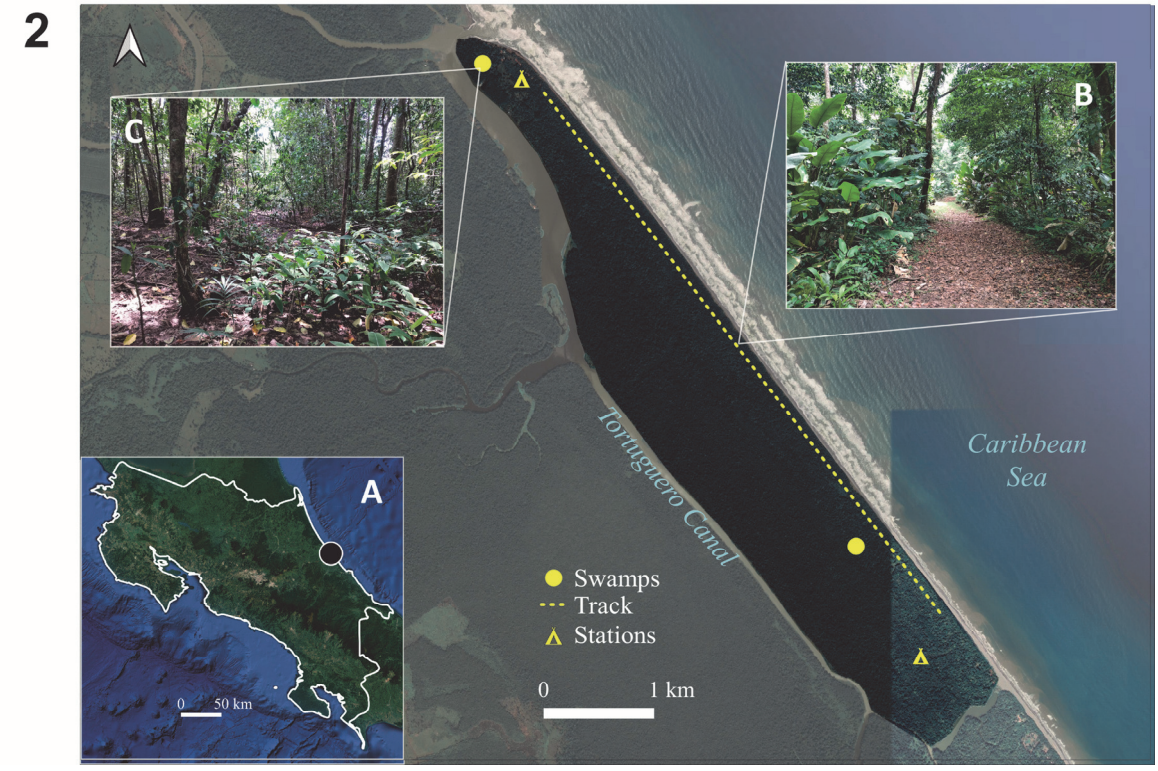


Fig. 1. *Cupiennius* spiders from Pacuare Nature Reserve. A) Cannibalism in *C. coccineus* B) Habitus of *C. coccineus*. C) Adult male of *Cupiennius getazi*, orange morphotype (photograph by P. Alonso). D) *C. getazi*, gray morphotype. **Fig. 2. Fig. 2.** Map of Pacuare Nature Reserve showing sampled areas. A) Location of Pacuare Nature Reserve. B) Main track of the reserve that connects the north and south stations. C) Swamp zone. / **Fig. 1.** Arañas *Cupiennius* de la Reserva Natural de Pacuare. A) Macho adulto de *Cupiennius getazi*, morfotipo naranja (fotografía de P. Alonso). B) Morfotipo gris de *C. getazi*. C) Canibalismo en *Cupiennius coccineus*. D) Hábito de *C. coccineus*. **Fig. 2.** Mapa de la Reserva Natural de Pacuare mostrando las áreas muestreadas. A) Localización de la Reserva Natural de Pacuare. B) Camino principal de la reserva que conecta los campamentos norte y sur. C) Zona de lagunas.

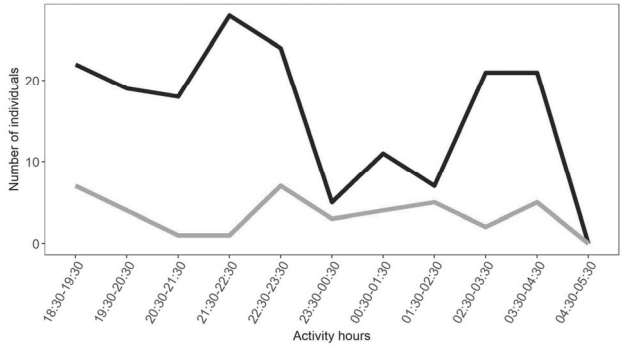


Fig. 3. Daily activity patterns of *Cupiennius* species from Pacuare Nature Reserve. The gray line represents *C. getazi* and the black line corresponds to *C. coccineus*. / **Fig. 3.** Patrones de actividad diaria de las especies de *Cupiennius* de la Reserva Natural de Pacuare. Las líneas grises representan a *C. getazi* y las negras a *C. coccineus*.

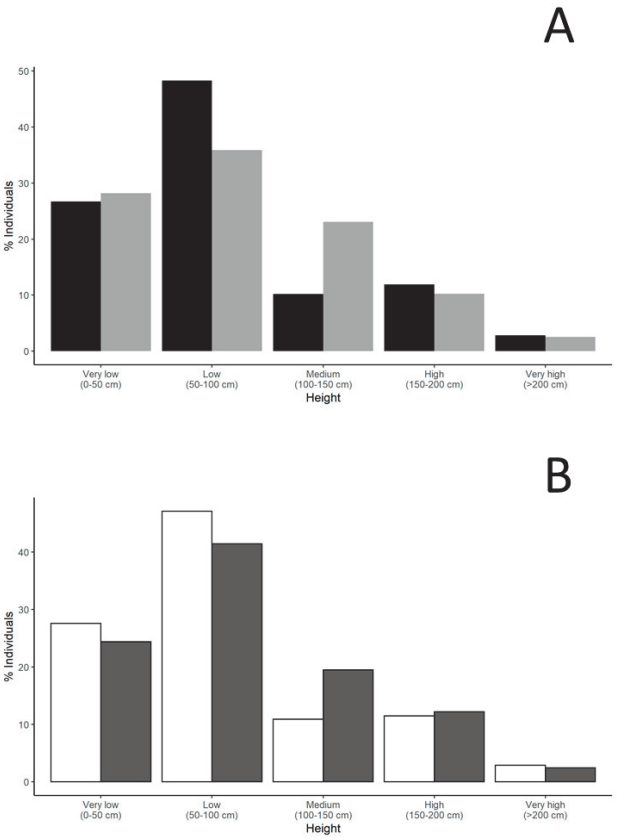


Fig. 4. Height location above the ground of *Cupiennius* species from Pacuare Nature Reserve. A) Interspecific comparison; gray bars represent C. *getazi* and black bars correspond to *C. coccineus*. B) Intraspecific comparison; empty bars represent adults/subadults and filled bars correspond to juveniles. / **Fig. 4.** Altura sobre el suelo a la que se encontraban las especies de *Cupiennius* de la Reserva Natural de Pacuare. A) Comparación interespecífica; las barras grises representan a *C. getazi* y las negras a *C. coccineus*. B) Comparación intraespecífica; las barras vacías representan a los adultos/subadultos y las llenas a los juveniles.

C. getazi was found within the forest in Lapinski & Tschapka (2018) work at Tirimbina Biological Reserve, corroborating that this species is restricted to early succession habitats (Lapinski & Tschapka, 2013). Pacuare Nature Reserve is a secondary tropical forest which was reforested 30 years ago, thus there is an early successional habitat with a poor tree density. Although both studied areas, the track and the swamp zones, presented a low tree density, a considerable width of the track is constantly deforested. This fact makes the track an early successional open area without trees, perfectly suitable for *C. getazi.* In addition, contrary to *C. coccineus*, C. *getazi* was frequently seen in the surrounding gardens of the camp stations (pers. obs.), suggesting that this species could be also widespread in disturbed environments. Our findings of habitat segregation in *Cupiennius* spiders are consistent with previous studies that show species-specific habitat preferences within different taxa of generalistic predators, for example in assemblages of lizards, frogs or spiders (Reagan, 1992; Dias & Brescovit, 2004; Menin et al., 2005) and how micro-habitat segregation and partitioning of foraging niches can facilitate coexistence of several species, as occur in many spiders (Nieto-Castañeda & Jiménez-Jiménez, 2009; Thompson et al., 2015; Villanueva-Bonilla et al., 2019).

The daily activity periods of the two species were similar, showing no allochrony. The activity patterns and the higher periods of activity for both species were based on four activity peaks every three hours approximately (Fig. 3). These results contrast with Schmitt et al. (1990) laboratory measurements of the daily locomotor activity patterns, where the maximum activity peaks for *C. getazi* were between 18:00 and 20:00, and for *C. coccineus* were between 21:00 and 00:00. Therefore, their observation that "*C. coccineus* spiders were most active when the activity of *C. getazi* was decreasing" was not observed in the field conditions. Schmitt et al. (1990) also reported constant activity of *C. coccineus* over the whole dark phase, whereas *C. getazi* was only active during the first 8 hours of the night. Contrarily to this, we found that *C. getazi* was also active during the whole dark phase. *Cupiennius* are low-cost sit-and-wait predators (Barth & Seyfarth, 1979), so they do not achieve a significant saving of energy by hunting for only part of the night, reducing even more its potential hunting success. The relatively low abundance of potential intraguild competitors, together with the spatial segregation of the species, makes it plausible that no species-specific hunting nighttime preferences have developed (Lapinski & Tschapka, 2013). Interestingly, although *Cupiennius* are nocturnal spiders, Schmitt et al. (1990) found that a small percentage (4.1% in males, 8.7% in females) of the total daily activity of *Cupiennius* spiders was in the light phase, consisting in small activity peaks between 15:00 and 16:00. According to this, a few individuals were seen outside their retreat during the day at Pacuare Nature Reserve, Gandoca-Manzanillo Wildlife Refuge (pers. obs.) and La Selva Biological Station (Barth et al., 1988). These observations could explain the small activity peaks in broad daylight registered in the Schmitt (1990) laboratory measurements.

Vertical distribution of the two species was similar, whereas between instars was significantly different. Both species show quite similar height ranges, with only small differences in the abundances of "medium" and "high" vegetation. The vertical distribution overlap of the species would increase the interspecific competence, in this way, habitat segregation reduces the number of interactions between them. Juveniles occurred lower than adults/subadults, who present a wider range of heights, although there was a partial overlap in "low" vegetation. The results regarding the vertical distribution segregation between the instars of *Cupiennius* spiders are the opposite to those evidenced by Lapinski & Tschapka (2018), where adults/subadults occurred lower than juveniles.

The vegetation dwelling spiders use nearly the whole height range, occurring even higher than had been estimated (Lapinski & Tschapka, 2018). Unfortunately, a total height range was probably underestimated in our study because most data could only be obtained by observation from the ground. Anyway, since both species are cannibalistic (Smith et al., 1992; pers. obs.) (Fig. 1A), as occur in other generalist spiders (Wagner & Wise, 1996), these subtle differences in vertical distribution would reduce intraspecific predation in *Cupiennius* spiders. In this framework, intraspecific differences in habitat use of the different instars have been reported in some spiders, such as the Theraphosidae *Ephebopus murinus* (Walckenaer, 1937) (Marshall & West, 2008) or the sympatric Ctenidae *Phoneutria fera* Perty, 1833, and *Phoneutria reidyi* (F.O.P.-Cambridge, 1897) (Torres-Sánchez & Gasnier, 2010).

Unlike *C. coccineus* (Fig. 1A-B), *C. getazi* have a wide range of conspicuous colouration based on orange or gray, comprising two different morphotypes (Barth, 2002) (Fig. 1C-D). Most of the observed individuals present the orange morphotype whereas only a few ones were grayish. As some studies in spiders have already suggested (Galiano, 1981; Gunnarsson, 1987), future analyses on heritability could determine the genetic systems involved in this process, and therefore increase our comprehension about the forces and selective pressures of the color variation in *C. getazi*.

Overall, the two sympatric *Cupiennius* spiders at Pacuare Nature Reserve showed clear differences in habitat selection (*C. getazi* dominates the track and *C. coccineus* the swamp zones), which limit the interspecific encounters. In addition, the instars exhibit vertical distribution segregation (juveniles occurred at lower vegetation than adults/subadults), which reduce the cannibalistic tendencies of *Cupiennius*. Our work also points to the importance of further lines of investigation regarding the conspicuous coloration of *C. getazi*.

Acknowledgements

We are deeply grateful to Marcos Méndez and an anonymous reviewer whose suggestions greatly improved the manuscript. We would like to thank Alberto Sánchez-Vialas and Mario García-París (Museo Nacional de Ciencias Naturales, MNCN-CSIC) for the help and comments on the manuscript, José Manuel Serrano Talavera (Universidad Complutense de Madrid, UCM) for his help designing the study, Luis Cayuela Delgado (Universidad Rey Juan Carlos, URJC) and Javier Blasco-Aróstegui for statistical advice and Pedro Alonso-Alonso for sharing his photographs. Field work was carried out with permits from the "Programa de Investigación ACLAC-SINAC-MINAE": R-SINAC-PNI-ACLAC-025-2019; Exp. Dig. N° M-PC-SINAC-PNI-ACLAC-023-2019.

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