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Niche differentiation of two sibling wolf spider species, *Pardosa lugubris* and *Pardosa alacris*, along a canopy openness gradient

Radek Michalko[1,2], **Ondřej Košulič**[3], **Vladimír Hula**[4] and **Kamila Surovcová**[3]: [1]Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, Brno 611 37, Czech Republic; [2]Department of Forest Ecology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 3, Brno 613 00, Czech Republic; [3]Department of Forest Protection and Wildlife Management, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 3, Brno 613 00, Czech Republic; [4]Department of Zoology, Fisheries, Hydrobiology and Apiculture, Faculty of Agronomy, Mendel University in Brno, Zemědělská 1, 613 00 Brno, Czech Republic. E-mail: ondra.kosulic@seznam.cz

Abstract. Phylogenetic niche conservatism can cause strong interspecific competition among closely related species leading to competitive exclusion from local communities or meta-communities. However, the coexistence of close relatives is often reported. One of the most frequent mechanisms mediating such coexistence is resource partitioning. Here, we investigated the niche differentiation of two sibling spider species, *Pardosa alacris* C.L. Koch, 1833 and *P. lugubris* Walckenaer, 1802, along a canopy openness gradient. We further investigated differences in body size as an additional axis for niche partitioning. We explored niche partitioning along the canopy openness gradient at eight locations. In each afforested location, 60-m-long transects were established consisting of five pitfall traps placed at regular 15-m intervals along the gradient. We measured the body size of individuals of both species collected at the gradient's extremes. We found that the two *Pardosa* species occurred syntopically but had clearly differentiated spatial niches along the canopy openness gradient. *Pardosa lugubris* displayed a preference for closed canopies in dense forest habitats and its abundance gradually decreased as the canopy opened while the opposite was the case for *P. alacris*. The two species also differed in body size. Each species was larger at its preferred gradient extreme than was the other species. The coexistence of the two *Pardosa* species was mediated mainly by spatial niche partitioning. Body size differences may represent another axis for niche partitioning.

Keywords: Coexistence, resource partitioning, spatial niche, body size, Lycosidae

Interspecific competition is considered to be one of the main ecological and evolutionary forces driving species composition and abundances of meta-communities (Chase & Leibold 2003). Classical niche theory predicts that two species with the same niche but having distinct competitive abilities cannot coexist at equilibrium when the resources are limited because the weaker competitor would be excluded (Gause 1934; Hardin 1960; Violle et al. 2011). In other words, each species needs to be limited more by itself than by heterospecifics in order to coexist (Chesson 2000). The most frequently stated mechanism that mediates coexistence is resource partitioning. In such cases, species differ in the resources that they use (e.g., diet, micro-habitat, light). Alternatively, species may differ in the time or place of their use of common resources (Chesson 2000).

Interspecific competition is considered to be rare or weak in spiders (Wise 1993). In closely related spiders, however, it can sometimes be sufficiently strong as to cause niche heterogenization, niche shifts, and even competitive exclusion (e.g., Spiller 1984; Nyffeler et al. 1986; Herberstein 1998; Marshall & Rypstra 1999; Miyashita 2001; Michalko & Pekár 2014). Interspecific competition is also one of the main forces that led to the adaptive radiation of tetragnathids on the Hawaiian Islands (Gillespie 2005).

Resource partitioning has been documented as the mechanism most frequently mediating the coexistence of spiders. With respect to trophic niches, spiders can utilize different prey types or sizes as an effect of different hunting strategies and/or body sizes (Olive 1980; Michalko & Pekár 2015). Temporal niche partitioning can be mediated by different diurnal activities or phenology (Tretzel 1954, 1955; Herberstein & Elgar 1994; Herberstein 1997). Spatial niche partitioning plays a very important role for spiders and can occur at a very fine scale (Scheidler 1989; Cumming & Weslowska 2004). Spider assemblages can be vertically or horizontally stratified due to different physiological tolerances, body sizes, and hunting strategies as well as distinct primary defence mechanisms (Richman et al. 1995; Wagner et al. 2003; Cumming & Weslowska 2004; DeVito et al. 2004).

Pardosa lugubris Walckenaer, 1802 and *P. alacris* C.L. Koch, 1833 (Lycosidae) are sibling species belonging to the *lugubris* species group. The *lugubris* group consists of four species in Central Europe: *P. lugubris*, *P. alacris*, *P. saltans* Töpfer-Hofmann, 2000 and *P. baehrorum* Kronestedt, 1999 (Töpfer-Hofmann et al. 2000). *Pardosa baehrorum* differs from the other three in habitat requirements as it lives in *Salix* grown around the Danube River. The other three species occur in very similar environmental conditions, but *P. saltans* is a western European species, while *P. lugubris* and *P. alacris* are distributed across the whole of Europe (Töpfer-Hofmann et al. 2000; Nentwig et al. 2015). Here, we focus on the latter two species, which are the most common species in deciduous forests in Central and Eastern Europe.

Both of the studied species are very similar and only males can be distinguished reliably on the basis of their morphological characters (Kronestedt 1992; Töpfer-Hofmann et al. 2000). Moreover, these two species often occur sympatrically (Buchar 1999; Buchar & Růžička 2002; Bryja et al. 2005; Košulič & Hula 2011). This raises the important question of how such coexistence is possible. It is hardly possible that the coexistence is mediated by trophic niche partitioning as the diets of

Table 1.—Characteristics of individual study sites located across South Moravia in the Czech Republic and abundances of *Pardosa alacris* and *P. lugubris* in each studied location.

Location	District	Latitude	Longitude	Altitude (m)	Age (years)	*P. alacris* / *P. lugubris*
Kuntínov	Břeclav	48°57′12.52″N	16°50′11.65″E	280	100–120	110 / 69
Jesličky	Břeclav	48°56′35.02″N	16°50′19.26″E	245	80–100	65 / 107
Kurdějov	Břeclav	48°58′58.93″N	16°46′4.41″E	305	90–110	18 / 34
Nedánov	Břeclav	48°56′43.20″N	16°50′55.71″E	325	90–110	104 / 76
Vranovice	Brno	48°57′25.56″N	16°35′46.07″E	205	100–120	72 / 57
Milovice	Mikulov	48°50′55.90″N	16°41′34.68″E	215	100–120	63 / 63
Mutěnice	Hodonín	48°52′51.23″N	17° 4′49.07″E	180	110–130	75 / 59
Dubňany	Hodonín	48°53′30.18″N	17° 7′10.71″E	204	110–130	114 / 85

Pardosa spiders generally overlap considerably (Suwa 1986). Moreover, the phenology of *Pardosa* spiders is also very similar (Tretzel 1954; Suwa 1986; Moring & Stewart 1994; Buchar 1999; Nentwig et al. 2015). Available data suggest that *P. lugubris* and *P. alacris* might have differentiated their niches along the light gradient but this idea had never been tested adequately. In the present study, we investigated the two sibling species' microhabitat preferences by establishing 60-m-long transects of pitfall traps along the canopy openness gradient at eight afforested locations. We also measured the sizes of the spiders as an additional dimension for niche partitioning. We hypothesized that the coexistence of *P. lugubris* and *P. alacris* is mediated mainly by niche differentiation along the light gradient.

METHODS

Studied species.—We studied two species of the genus *Pardosa* (Lycosidae): *P. alacris* and *P. lugubris*. They are closely related species of the *lugubris* group and have very similar morphological and ecological characteristics. Only adult males can be distinguished according to the shape of their tegular apophyses and the colour of their cymbium, while adult females of the two species are almost identical (Töpfer-Hofmann & von Helversen 1990; Kronestedt 1992, 1999). The two species also differ in courtship behaviour (Vlček 1995; Töpfer-Hofmann et al. 2000; Chiarle et al. 2013). These species have Eastern Palaearctic (*P. alacris*) and Palaearctic (*P. lugubris*) distributions (World Spider Catalog 2015). Both of the studied species prefer deciduous forests (except dense beech forest), forest–steppe areas, and forest edges but without any specific environmental characteristics (Buchar & Růžička 2002). They belong to the ground hunters guild and employ a sit-and-move hunting strategy (Samu et al. 2003; Cardoso et al. 2011). *Pardosa alacris* and *P. lugubris* are very common in the Czech Republic and frequently have sympatric occurrence (Buchar 1999; Buchar & Růžička 2002).

Study area.—The study was conducted at eight locations across South Moravia at the northern-most edge of Pannonia in the Břeclav, Brno, Mikulov, and Hodonín districts (Table 1). All study locations were afforested with *Quercus robur, Q. petraea*, and *Carpinus betulus* as the main tree species with a mixture of xerothermophilous *Q. pubescens* (*Q. pubescens–Q. petraea* plant communities). All study sites had similar altitudes and comparable forest growth ages (former coppiced forests) and are now not actively managed or disturbed by humans (Table 1).

Data collection.—We established 60-m-long transects reflecting the canopy openness gradient in each of eight forest stands. Each trap location differed in light density from the most open and sparse canopy (forest steppe clearings) to the most closed and dense canopy (dense forest habitat). Each transect consisted of five pitfall traps placed at regular intervals. Each pitfall trap consisted of a plastic cup (9 cm in diameter, 15 cm long) sunk so as to be flush with the soil surface and filled with 4% formaldehyde solution as a killing and preserving agent. In total, there were eight transects and each level of canopy openness was therefore represented eight times. Spiders were collected from 12 May to 14 July 2012. Adult males were used for analyses as they can be easily determined and collected during the early summer period (Kronestedt 1992, 1999). We selected this period because it is when both species reach the peak of their activity in Central Europe and it could be expected that all specimens would be adult (Buchar 1999). All examined material was deposited in the public collection of the Mendel University, Faculty of Foresty and Wood Technology in Brno. The numbers of collected specimens in each studied locality are shown in Table 1 and the raw data can be found in Supplemental 1 (online at http://dx.doi.org/10.1636/M15-46.s1).

The light volume gradient was calculated using imaging software (GAP Light Analyzer, version 2.0) for extracting canopy structure and gap light transmission indices from true-colour fisheye photographs. Each fisheye photograph was taken from ground level around the pitfall traps during material collection (14 July 2012). The date was selected because the canopy is the densest during this period.

Statistical analyses.—All analyses were performed within the R environment (R Development Core Team 2015) with R packages "geepack" (Højsgaard et al. 2006) and "nlme" (Pinheiro et al. 2015). Niche overlap (NO) was calculated using kernel density estimation (see Geange et al. 2011). The index has values ranging from 0 (no overlap) to 1 (complete overlap). We performed null modelling to test whether the two *Pardosa* species occupied significantly distinct niches because deviance from 1 may be caused purely by chance (Geange et al. 2011). Because we collected the data at eight locations, we calculated NO for each location separately and present here mean NO and its standard error. We performed 1000 permutations for each location. We employed the Bonferroni correction to minimize the probability of type I errors and we considered the significance level to be $\alpha = 0.00625$ for distinct niche occupancy. To investigate the change in the spatial distribution of the two *Pardosa* species along the canopy openness gradient, we calculated for each location the proportions of individuals that were caught in each trap. The changes in proportions along the openness gradient were studied using generalized

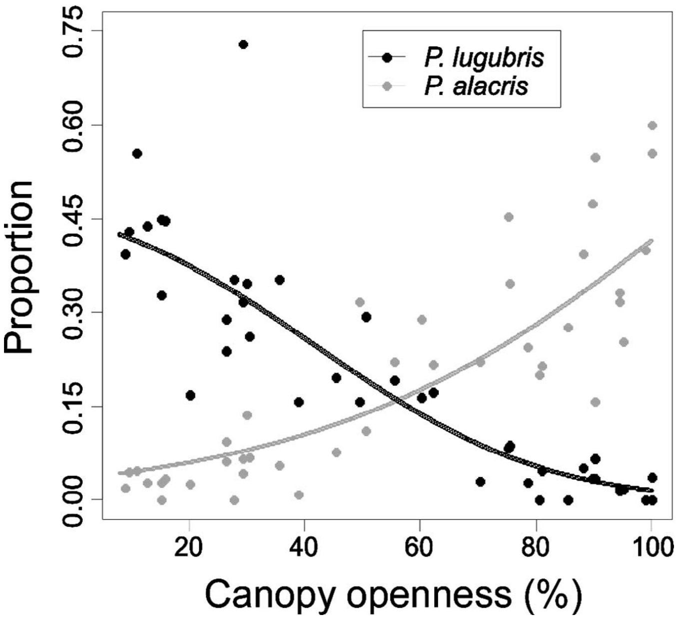

Figure 1.—Relationship between canopy openness and relative abundances of two *Pardosa* species.

estimating equations (GEE) with binomial error structure and logit link (GEE-b) as an extension of generalized linear models for correlated data. GEE was used because the samples were taken at eight different localities (Pekár & Brabec 2012). Because the traps in each locality were situated at regular 15-m intervals, we used the 'AR1' correlation structure where the correlation between each two traps decreases with increasing distance between the traps. The *Pardosa* species' niche width along the canopy openness gradient was estimated using the Shannon diversity index (H), which was calculated for each location separately. Because there were five traps per locality, the index can reach values from 0 to 1.61. The degree of specialisation depends on the choice of a researcher (Futuyma & Moreno 1988). We therefore defined the stenovalence as H = 0–0.54, oligovalence as H = 0.55–1.07 and euryvalence as H = 1.08–1.61. Niche width was compared using linear mixed effects models (LMEs) where species and location acted as fixed and random effects, respectively.

To explore whether the distribution of the two *Pardosa* species could be explained also by interspecific competition, we employed a static approach for calculating the coefficients of competition from census data where species abundances are regressed against one another (Pfister 1995; Fox & Luo 1996). Significant negative slope parameters then indicate (not prove) the presence of interspecific competition. However, as negative relationships may arise from distinct requirements of environmental conditions rather than from interspecific competition, environmental conditions need to be incorporated into the model's predictor (Pfister 1995; Fox & Luo 1996). Species abundances should be also standardized as estimations of competitive coefficients are dependent on population variance and thus could produce statistical artefacts (Fox & Luo 1996). Competition coefficients were studied using LMEs where the standardized abundances of the potential competitor and canopy openness acted as fixed effects and location acted as a random effect. We used the 'varIdent' and 'varExp' variance functions to deal with heteroscedasticity (Pekár & Brabec 2012).

To compare size differences, we selected 8–10 individuals from each species from six locations ($n = 117$). Individuals were selected so that both gradient extremes (open and closed canopy) were represented by 4–5 individuals. Individuals within these groups were selected randomly without replacement. We compared the sizes of the two species using a GEE with gamma error structure and log link (GEE-g) since size can be considered as having the gamma distribution and the data were auto-correlated (Pekár & Brabec 2009, 2012). Species, habitat type according to canopy openness, and the interaction between these two factors acted as the explanatory variables while location acted as a grouping variable. We used an 'exchangeable' correlation structure because the relationship among individuals within the grouping variable was blocked (Pekár & Brabec 2012).

RESULTS

In total, 1171 adult spiders from the *P. lugubris* group were collected. Out of these, 621 specimens belonged to *P. alacris* and 550 specimens belonged to *P. lugubris* (Table 1).

The two *Pardosa* species occupied distinct environmental niches (mean NO = 0.27, SE = 0.11, null model, 1000 permutations, $P < 0.001$). The proportions of *P. alacris* increased (GEE-b, $\chi^2_1 = 43.9$, $P < 0.001$, Fig. 1) and those of *P. lugubris* decreased (GEE-b, $\chi^2_1 = 196$, $P < 0.001$, Fig. 1) with canopy openness. Both species were euryvalent (*P. alacris*: H = 1.23, SE = 0.06; *P. lugubris*: H = 1.18, SE = 0.06) and we were not able to reject the null hypothesis for niche width differences between the two species (LME, $F_{1,7} = 0.4$, $P = 0.55$).

Pardosa lugubris abundance had a significant positive effect on *P. alacris* abundance (LME, $F_{1,29} = 43$, $P < 0.0001$, slope parameter $\beta = 0.8$), but *P. alacris* abundance did not have a significant effect on *P. lugubris* abundance (LME, $F_{1,29} = 2.7$, $P = 0.11$, slope parameter $\beta = 0.9$).

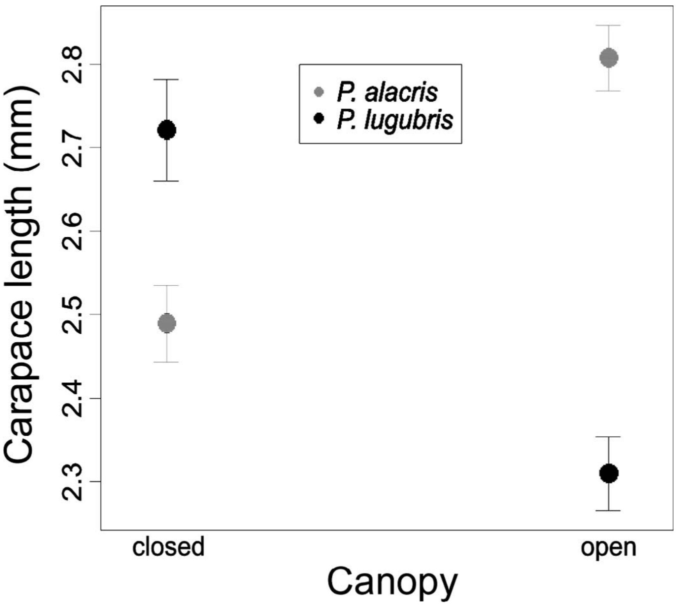

Figure 2.—Size comparison between two *Pardosa* species from two habitats with distinct levels of canopy openness. Points are means and line segments are SE.

There was a significant difference in carapace length between the two species (GEE-g, $\chi^2_1 = 5.6$, $P = 0.0184$, Fig. 2) as well as significant interaction between species and habitat type (GEE-g, $\chi^2_1 = 44.9$, $P < 0.0001$, Fig. 2). *Pardosa alacris* was larger in clearings than it was in forests (contrasts, $P = 0.0002$) while the opposite was true for *P. lugubris* (contrasts, $P < 0.0001$). In clearings, *P. alacris* was larger than *P. lugubris* (contrasts, $P < 0.0001$), while the opposite was true in forests (contrasts, $P < 0.0001$). *Pardosa alacris* from clearings was larger than was *P. lugubris* from forests (contrasts, $P < 0.0001$).

DISCUSSION

In the present study, we studied the spatial niche partitioning between two sibling *Pardosa* species, *P. lugubris* and *P. alacris*. We found that even though these lycosids are euryvalent and occur syntopically, they had clearly distinguished niches along the canopy openness gradient. The relative abundance of *P. alacris* gradually increased with openness while the opposite was true for *P. lugubris*. Thus, niche differentiation along the canopy openness gradient mediated the coexistence of these two species in meta-communities. Horizontal stratification is a frequently reported mode of niche differentiation among wolf spiders and even *Pardosa* species. For example, Suwa (1986) found that four *Pardosa* species occurring in Hokkaido in Japan were clearly separated in space. Species with similar habitat preferences are separated geographically and occur allotopically in overlapping areas. In contrast, species with distinct habitat preferences evince high geographical overlap. Moring & Stewart (1994) found that six *Pardosa* species that occur syntopically had clearly segregated spatial niches among five distinct habitats that represented successional plant zones along a stream.

It is unlikely that current interspecific competition is the process behind the distribution pattern of *P. alacris* and *P. lugubris* since no significant negative relationship between their abundances was observed after taking environmental factors into account. Instead, there was a positive relationship between their abundances when *P. alacris* abundance acted as an explanatory variable. This positive relationship suggests that these species respond similarly to some landscape features. The distribution pattern is therefore most likely influenced by distinct physiological tolerances, but this assumption needs to be tested.

There was an interesting pattern in size distribution between the two *Pardosa* species. Conspecific males from suitable conditions were larger than were heterospecifics for which the conditions were less suitable. *P. lugubris* males were larger than *P. alacris* males under closed canopies, while *P. alacris* males were larger under open canopy conditions. This pattern may have been caused by several not mutually exclusive factors. Smaller or less competitively capable males might have been pushed by intraspecific interactions (competition for mates, food, etc.) into less favourable conditions. Interspecific interactions might also have contributed to this pattern. Nevertheless, the size difference between the two lycosids could also represent an additional axis for niche differentiation, e.g., trophic niche. Although the *Pardosa* spiders utilize very similar prey types, body size differences can lead to trophic niche partitioning with respect to prey size (Suwa 1986; Michalko & Pekár 2015).

In summary, we found that the coexistence of the two sibling species, *Pardosa alacris* and *P. lugubris,* is mediated by spatial niche separation. Although both species can occur syntopically, *P. alacris* preferred open canopies while *P. lugubris* preferred closed canopy habitats. The distribution of the two *Pardosa* species is most probably caused by distinct requirements for environmental conditions. The two lycosid spiders differed in body sizes, which could represent an additional axis for niche partitioning. Nevertheless, it should be noted that our results have a rather local relevance and apply only to the studied region. The distribution pattern of the *Pardosa* species from the *lugubris* group can differ among various regions. Therefore, further study is needed to explore how the overall coexistence of these species is mediated at their common distribution range.

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