Impact of Habitat Complexity on Body Size of Two Spider Species, *Alopecosa cuneata* and *A. pulverulenta* (Araneae, Lycosidae), in River Valley Grasslands

Marzena Stańska¹, Tomasz Stański¹, Ewelina Wielgosz², Izabela Hajdamowicz¹

¹Siedlce University of Natural Sciences and Humanities, Faculty of Natural Science, Department of Zoology, B. Prusa 12, 08-110 Siedlce, Poland
²Warszawska 80A, 21-400 Łuków, Poland

Received: 9 April 2017
Accepted: 11 July 2017

Abstract

Many studies have shown that vegetation structure and habitat complexity affect taxonomic composition, functional diversity, and the number of individuals in spider assemblages. These factors also affect spider body size, but mechanisms responsible for that are still not well understood. In our research, we examined the relationship between the body size of spiders from two species – *Alopecosa cuneata* and *A. pulverulenta* – and environmental factors such as habitat type and habitat complexity. Our research was conducted in the Bug River Valley on 12 plots covering three types of habitats: mesic meadow, sandy grassland, and xerothermic grassland. Spiders were collected in 2007-08 from April to mid-November using pitfall traps. In total we measured 334 males and 168 females of *Alopecosa cuneata* and 315 males and 104 females of *A. pulverulenta*. The generalized linear mixed model revealed that individuals of *Alopecosa cuneata* as well as *A. pulverulenta* reached larger sizes in more complex vegetation, whereas the habitat type did not affect the spider body size. One of the likely mechanisms responsible for a larger body size in more complex habitats is predator pressure. Birds as the main predators of spiders, being selective in their choice of prey, may collect larger spiders with higher intensity than smaller ones. We suggest that more complex habitats with dense vegetation provide better shelter for large spiders, which allows them to avoid predators. Our results indicate that habitat complexity may be an important determinant of body size distribution in spider assemblages.

Keywords: spider body length, epigeic spiders, vegetation complexity, body size distribution

*e-mail: marzena.stanska@uph.edu.pl*
Introduction

Body size is correlated with many physiological and ecological processes as well as organism’s traits, e.g., metabolic rate [1], life duration [2], predation [3], parasitism [4], and competition [5]. Current knowledge of mechanisms affecting the body size distribution is based mainly on studies involving vertebrates [6-9], while researches on invertebrates are still rare, although more frequent during last years [10-15]. Many of these studies analysed body size patterns of a particular group of invertebrates on a large geographical scale like a continent [10, 12-14], whereas knowledge about mechanisms affecting body size distribution on a local scale are still limited [11, 16-17].

Spiders are an excellent group of organisms to study mechanisms responsible for body size distribution, both on large geographical and local scales. They occur in large numbers in most habitats and they are very sensitive to habitat structure and microclimatic conditions [18]. Many studies have shown that complexity and structure of habitat (which often comes down to vegetation structure and density) had a significant influence on the abundance, species richness, and distribution of spiders [19-23]. Despite the great number of research on spider-habitat interactions, only limited studies have included body size. On a large geographical scale, i.e., Europe, Entling et al. (2010) showed that the mean body size of spider assemblages increased from cool and moist to warm and dry environments [12]. Research by Drapela et al. (2011) revealed that landscape structure (e.g., distance to the nearest woody area) affected the body size of Pardosa agrestis – one of the most abundant spiders in arable fields [24]. Gibb et al. (2015) studied the impact of climate and habitat factors on morphological traits of foliage-living spiders in grassland in Australia [25]. They found a relationship between some morphological traits of spiders (e.g., body length, fang length, asymmetry) and environmental factors (elevation, latitude, longitude, annual mean temperature). Moreover, some authors have conducted experiments consisting of the manipulation of habitat complexity and proved that in a more complex habitat (i.e., with more dense vegetation), spiders are larger [26-27]. However, the mechanisms responsible for the increase in spider body size in more dense and complex habitats are poorly understood. One of the reasons for this phenomenon is the pressure of predators. Spiders are particularly exposed to predation by birds [28], who while searching for prey usually choose more conspicuous (i.e., larger) spiders [29-31].

In this paper, we analysed the relationships between the body size of two spider species and environmental factors such as habitat complexity and the type of habitat in the Bug River Valley in eastern Poland. According to McCoy and Bell (1991), habitat complexity can be defined as absolute abundance (per unit area or per unit volume) of individual structural components, but precise definition depends on a spatial scale at which it is examined [32]. In our research, habitat complexity reflected the degree of surface cover by vegetation in different height classes. We chose two model species belonging to the Lycosidae family: Alopecosa cuneata (Clerck, 1757) and A. pulverulenta (Clerck, 1757). Both analysed species are common in Europe and Poland and can be found mainly in open areas [33-35]. Alopecosa cuneata in central Europe inhabits mostly oligotrophic grasslands, fresh meadows, forest edges, vineyards, and ruderal areas [35]. A. pulverulenta has a wider habitat amplitude than A. cuneata and occurs on oligotrophic grasslands, fresh and moist meadows, raised bogs, forest edges, and coastal habitats [35-36]. None of the two species builds a hunting web. Instead, they actively hunt on the ground.

We proposed a hypothesis that body size of the studied spider individuals increases together with increasing habitat complexity in line with the results obtained by the above-mentioned authors [26-27]. We also expected a difference in the body size of spiders between the analysed habitats (mesic meadow, sandy grassland, and xerothermic grassland).

Material and Methods

Study Sites

The research was conducted in the Bug River Valley (a large lowland river in Eastern Poland, 52°41’32.14”N, 21°52’57.07”E, 52°16’53.15”N, 23°08’35.44”E) at 12 study plots located near the villages of Mogielnica, Morzyczan, Płatkownica, Zabuże, and Gnojno. Our research covered three types of habitats in the valley: mesic meadow (four plots), sandy grassland (four plots), and xerothermic grassland (four plots). Mesic meadows (Poo-Festucetum) developed in the upper alluvial terrace were located in Mogielnica, Morzyczan, Płatkownica, and Zabuże. Xerothermic grasslands occurred on the slopes at the edge of the valley (Adonido-Brachypodietum in Gnojno and Mogielnica), and on the slopes of flood banks (Tunico-Poetum compresse in Morzyczan and the Agropyretetem intermedio-repentis class in Płatkownica). Sandy grasslands (Diantho-Armerietum in Gnojno and Płatkownica, Sclerantho-Herniarietum glabre in Morzyczan, Sileno-Festucetum trachypyllae in Mogielnica) were distributed in a mosaic of meadows at different distances from the river bed. Plant communities were named after Załuśki (1995) and Matuszkiewicz (2005) [37-38].

Habitat Complexity

Measurements of habitat complexity were carried out at each study plot every time the material was collected. We assessed the vegetation cover in four height classes: 1) lower layer (0-10 cm), 2) low layer (10-30 cm), 3) middle layer (30-50 cm), and 4) high layer (above 50 cm). A 1 m² wooden frame was used to measure the vegetation cover in three randomly selected places at each plot. The area of the frame was divided into 16 smaller quadrats to facilitate
the measurements. The percentage of each vegetation class was estimated in each quadrat and a numerical scale was established: 0 for 0%, 1 for 1-25%, 2 for 26-50%, 3 for 51-75%, and 4 for 76-100%. The mean value was calculated for the whole area of the wooden frame and measurements from three samples were averaged. The resulting figure was the index of vegetation complexity, which can be defined as summed indices of cover degree of vegetation in different height classes. The index was determined for each sample when spider material was collected.

Spider Samples and Data Analyses

The material was collected in 2007-08 from April to mid-November using pitfall traps. Ten pitfall traps were placed in the ground along a straight line at a distance of two metres on each study plot. Each trap was filled to one-third of its volume with the preservative liquid propylene glycol. In order to reduce the surface tension of the liquid and prevent spiders from escaping, a detergent was added. The pitfall traps were emptied fortnightly. The material was sorted and spiders were identified to the species level. Adult individuals of *Alopecosa cuneata* and *A. pulverulenta* found in samples were measured from the front margin of the cephalothorax to the hind end of the abdomen using the Cool View computer program with an accuracy of 0.01 μm. This value (total length of cephalothorax and abdomen) was defined in our study as body size. Damaged and immature individuals were excluded from the measurements.

Prior to all analyses, the body size of spiders were log-transformed. Based on the conducted measurements, we calculated the mean body size separately for males and females belonging to two analysed spider species for each study plot for each date when material was collected. Each of the resultant values was considered one record.

To assess the effects of vegetation complexity and the type of habitat on spider body sizes, the generalized linear mixed model GLMM was used. Prior to analysis, variables were checked for normal distribution by the Shapiro-Wilk test. The variables “sex” (male vs. female) and “habitat” (mesic meadow, sandy grassland, and xerothermic grassland) were treated as qualitative factors. GLMM was used because data were collected on five study plots, which could be potentially different in terms of some factors (not included in analysis) influencing the body size of two analysed species. Taking into consideration this issue, “place” (one of the five particular places where spiders were collected) was included in analysis as a random variable. Statistical analyses were carried out using the StatSoft software STATISTICA. Results with p<0.05 were considered statistically significant.

Results

In total, 334 males and 168 females of *Alopecosa cuneata* and 315 males and 104 females of *A. pulverulenta* were measured. The GLMM analyses showed that the body size of *Alopecosa cuneata* as well as *A. pulverulenta* was determined by sex and habitat complexity, whereas the habitat type and place had no influence. Interactions between the analysed variables were not statistically significant (Tables 1-2). Females were larger than males in both analysed species (Fig. 1). The mean body size of *A. cuneata*, calculated for particular samples, ranged from 5.7 mm to 8.6 mm in the case of males and from 7.0 mm to 10.3 for females. The mean body size of *A. pulverulenta* varied between 5.6 and 7.0 mm for males and 5.2 and 9.0 mm for females.

The mean body size of both *Alopecosa cuneata* and *A. pulverulenta* increased with the increasing index of habitat complexity (Figs 2-3, respectively).

Discussion

Among the factors affecting spider assemblages – temperature, humidity, and availability of prey [39-41] –
habitat structure seems to be one of the most important. It
determines taxonomic composition, functional diversity,
and the abundance of spiders [19, 21, 41-42]. On a scale
relevant for spiders, habitat structure is determined
mainly by vegetation (or sometimes even by a single
plant), which provides spiders with a decent level of
humidity, shelter, abundance of prey, and sufficient
structures for building webs [22-23, 43]. Structurally
more complex habitat increases the number of spiders,
spider species, and species diversity [19, 22, 44].
Moreover, field experiments showed that individuals of
spiders are larger in such habitats. For example, Halaj
et al. (2000) conducted an experiment in which they altered
needle density and branching complexity of Douglas-fir
canopies and found that the body length of some spider
species increased in structurally more complex habitats
[27]. Sundberg and Gunnarsson (1994) showed that the
density of large (length≥2.5 mm) spiders was reduced on
branches with a removed portion of needles compared
to control branches, while such a relationship was not
observed in the case of small spiders [26]. Our results
support the findings of these authors. We showed that
habitat complexity positively affected the body size of
both analysed spider species.

There may be several mechanisms responsible for
a larger size of spiders in habitats with a more complex
vegetation structure. Organisms of a given species tend to
be large because larger individuals, among other things,
often have higher reproductive fitness and are better
adapted to environmental conditions [45-47]. Some of
these conditions, like humidity and shading, may be
crucial for spiders’ body size. Both are strictly connected
with vegetation, which maintains habitat humidity and
provides a shadow that protects organisms against water
loss. Larger spiders have greater resistance to desiccation
compared to small ones, which lose water at a higher rate
and thus reducing their survivorship [46, 48]. Therefore,
smaller spiders should occur in more humid habitats,
which very often means more dense vegetation. Such
regularity was observed by Entling et al. (2010) when
taking into consideration the mean body size for whole
assemblages based on the size of particular species [12].
They revealed that the mean body size of spider species
in Europe decreases from warm and dry to cool and moist
environments. In our study, conducted at the level of an
individual, rather an opposite tendency was observed.
Individuals of both A. cuneata and A. pulverulenta were
larger in more complex and hence probably more humid
habitats.

The next factor affecting spider body size is the
availability of prey, which is also connected with
vegetation and habitat complexity. For example, Halaj
et al. (2000) revealed that the abundance of Psocoptera
and Collembola, which are typical spiders’ prey, was
greater in a more complex habitat [27]. Spears and
MacMahon (2012) also found more prey items in shrubs
with high foliage density compared to low foliage
density [39]. Diehl et al. (2013) showed that the order
richness of spiders’ prey increased with plant diversity
and vegetation coverage [23]. Size, type, and abundance of potential prey available in habitats may be translated into size of predators, i.e., spiders. The large increase in prey consumption by spiders can reflect the increase in their body size [49]. Moreover, the body size of spiders and their prey are significantly correlated and generally spiders prefer prey smaller than 80-100% of their own size [50-51]. In general, smaller organisms should prefer habitats with a higher nutritional value of the potential food, because energy costs of obtaining food in sparse habitats exceed nutritional benefits [52-53].

Finally, one of the most important factors affecting body size distribution in animal assemblages is predation. Predators choose their victims selectively and such selection may be based on colour, behaviour, sex, or size [28, 54-57].

The main predators of spiders are birds [28, 58]. Gunnarsson’s (1998) field experiment clearly showed that spiders were considerably more abundant on branches protected against birds compared to control branches exposed to bird predation [31]. The importance of birds as a factor affecting the abundance and diversity of spiders (and indirectly the mean body size) was also stressed by Kozlov et al. (2015), who suggested that the impact of birds on spider assemblages was stronger than climate [59]. Unfortunately, studies analysing the impact of bird predation on spiders usually refer only to forests [28].

Birds use their eyesight when searching for prey, thus larger – i.e., more conspicuous – spiders are more exposed to such prey [29-31]. Both Alopecosa cuneata and A. pulverulenta are strongly exposed to predation because the impact of bird predation on actively preying spiders is much stronger compared to spiders building webs [60]. Sometimes the behaviour that increases the chances of being preyed may be closely related to sex. For example, smaller but roving males of Nephila clavipes suffered a higher mortality rate than larger and sedentary females [61]. On the other hand, a study concerning Pardosa milivina (which belongs, like our model species, to the Lycosidae family) revealed that males had lower survival rate than females, although both sexes exhibited similar levels of activity [62]. In the case of the two analysed spider species, males were more active, which proves that their large number compared to females collected in our study. Therefore, they were potentially more exposed to predation; but on the other hand, females were larger, which also increased their chances to be prey. It seems obvious that habitats with more complex structure provide better protection against predators (i.e., birds) for large spiders. As the conducted study revealed, the predation rate is lower in more complex habitat [63] and, moreover, vegetation structure may influence behaviour of birds during foraging [64]. Sundberg and Gunnarsson (1994) found that branches with a removed portion of needles had lower density of large spiders compared to the control branches [26]. This phenomenon was not confirmed in the case of small (below 2.5 mm) spiders. Gunnarsson’s study (1998) showed that the body size of Ptychohyphantes phrygianus (Linyphiidae family) was smaller on branches exposed to bird predation compared to the control, net-enclosed branches, but only in spring and not in autumn [31]. The importance of structurally complex habitat as a refuge from predators especially confirmed research on water organisms. For example, the study of Chydorus sphaericus species belonging to Crustacea revealed that larger specimens occurred among macrophytes, and the smallest ones were in the open water zone, which indicated that vegetation was a significant refuge against predators [65].

Conclusions

The results of our study demonstrated that the body size of spiders inhabiting grasslands was affected by habitat complexity. Individuals from two species, Alopecosa cuneata and A. pulverulenta, were larger in a more complex habitat, i.e., with more dense and structurally complicated vegetation. Several mechanisms may determine the body size patterns in spider assemblages, e.g., different microclimatic conditions, availability and size of prey or predation by birds. We suggested that the latter factor is the most crucial one. More complex habitats probably provide better shelter for large spider individuals, which allows them to avoid predators.

Acknowledgements

We would like to thank the people who contributed to our field and laboratory work, particularly Maria Oleszcuk, Łukasz Nicewicz, Rafał Oskroba, Michał Rzewuski, and Paweł Skorupka. The results of the research carried out under the research theme No. 222/05/S were financed from the science grant granted by the Ministry of Science and Higher Education.

References

races suggests competition between these sympatric snakes. J. Zool. 289 (2), 86, 2013.
17. WARZECZA D., DÍEKÖTTER, WOLTERS V., JAUKER F., Intraspecific body size increases with habitat fragmentation in wild bee pollinators. Landscape Ecol. 31 (7), 1449, 2016.
42. PLATEN R., BERGER G.  The impact of structural and landscape features of set-asides on the spiders (Araneae) of the herb layer. J. Arachnol. 41 (2), 143, 2013.
47. KAPUSTIANSKIJ A., STREINZER M., PAULUS H.F., SPAETHE J. Bigger is better: implications of body size for flight ability under different light conditions and the evolution of alloteism in bumblebees. Funct. Ecol. 21 (6), 1130, 2007.
64. POWOLNY T., ERAUD C., MASSON J.-D., BRETAGNE-LOLLE V. Vegetation structure and inter-individual distance affect intake rate and foraging efficiency in a granivorous forager, the Eurasian Skylark Alauda arvensis. J. Ornithol. 156 (3), 569, 2015.