Geographical sexual size dimorphism in an ant-eating spider, *Zodarion rubidum* (Araneae: Zodariidae)

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Abstract

Within-species variation in body size of males and females of an ant-eating spider *Zodarion rubidum* was studied by analysing 15 populations across Europe. The relationship between the body size of both sexes was allometric with female-biased sexual size dimorphism. Body size of males did not change with latitude or temperature, while that of females changed significantly with temperature. Larger females were found in regions with higher temperature which is presumably a result of an optimal climate: higher temperature and longer season provide higher prey availability which accelerates the growth rate of females, leading to a larger body size. As female size varied more than male size, a sexual size dimorphism cline was observed in *Z. rubidum*. Larger sexual size dimorphism was found in warmer regions. These results thus suggest that environmental conditions (temperature) influence intraspecific variation in sexual size dimorphism in *Z. rubidum*.

Keywords: *Araneae*, latitude, *sexual size dimorphism*, temperature, *Zodariidae*, Zodarion

Introduction

In many invertebrates adult females are larger than adult males (Fairbairn 1997). Recently, there has been a lot of discussion on the selective pressures that resulted in sexual size dimorphism (SSD) in spiders. It has been agreed that the large size in females is a result of selection for higher fecundity, while the small male size is a result of sexual selection (e.g. Head 1995). Despite this general agreement, a controversial discussion arose concerning pressures that caused extreme SSD in spiders. Vollrath and Parker (1992) suggested that SSD is a result of male dwarfism. According to their model, dwarf males are selected from weaker intrasexual competition that results from high mortality of males during the search for females. But Prenter et al. (1997) failed to find evidence for this model. In turn, they agreed with Coddington et al. (1997) that the SSD in European spiders might rather be explained by female gigantism that has evolved in order to attain large fecundity. Later Hormiga et al. (2000) came to conclusion that SSD in araneid spiders could be explained by several different evolutionary routes, including both aforementioned models. Whatever
the routes were, none of these hypotheses aimed to explain the variation in SSD between species. Only very recently, Moya-Laraño et al. (2002) showed that a simple biomechanical model accounted for the variation in SSD of web-building species: small males are selected in species where females occur in higher strata as the small weight facilitates climbing.

The majority of discussions concerned evolutionary mechanisms underlying interspecific SSD. Little attention has been paid to intraspecific (within-species) variation in body size in invertebrates, particularly spiders (Ashton 2001). Yet it is known that beside evolutionary pressures, ecological and physiological constraints affect body size and mediate variation in SSD (Head 1995). If the constraints possess different selecting pressures on males than on females along latitude then a geographical variation in SSD should occur.

Among spiders, intraspecific variation in body size has been studied only in two web-building species. Studies on a colonial Metepeira spinipes F. O. P.-Cambridge (Araneidae), occurring in three different types of habitats of North and Central America, revealed that the body size of females decreased with decreasing temperature (Benton and Uetz 1986; Piel 1996). Higgins (2000) found a similar pattern for another web-building spider, Nephila clavipes (Linnaeus) (Tetragnathidae): females were largest in warmer sites and smallest at cooler sites.

We have been studying geographical change in adult body size of a roaming ant-eating Zodarion spider. Species of this genus are native to the Mediterranean, particularly to the Iberian Peninsula. However, one species, Zodarion rubidum Simon, has spread over Europe during the last decades. At the beginning of the last century it was known only from southern France, later came records from northern France; and since the 1970s also from other western, central and eastern European countries. Nowadays it occurs nearly up to the Baltic sea in the north and Ukraine in the east (Pekár 2002). Such a large area of distribution allowed us to compare male and female body sizes across an almost 2000 km long area extending from southwest to northeast Europe. It was found that body size, and particularly SSD, changed providing evidence that males and females of Z. rubidum possess different sensitivity to environmental conditions, particularly temperature, during growth.

Material and methods

Due to financial limits we could not sample Zodarion rubidum spiders on our own and obtain a balanced data set with continual distribution along the north–south gradient. Thus we had to work with the material deposited in personal or museum collections. Altogether we obtained material of 15 spider populations across Europe (Figure 1) that was composed of 158 adult male and 161 adult female spiders (Table I). This amounts to more than 90% of all sites where this species has been found so far (Pekár 2002). The spiders were collected in different years over the last four decades.

We used only adult spiders in this study. In each spider the length of the prosoma was measured under a binocular microscope. This measure was chosen because it is constant over the adult stage and is not affected by the current nutritional state of the spider.

Two explanatory variables, latitude (i.e. coordinates of the study sites) and temperature (long-term annual average), were used to explain the observed pattern (Table I). Although another factor, altitude, might have an important effect, values of this variable could not be obtained for all sites. As no data on the development of this spider are known (such as lower developmental threshold), other measures of the temperature though being more relevant to the size pattern could not be used. Most of the data on average annual temperature were obtained from WorldClimate (2004). Data on sites in Slovakia were provided by the Slovak
Figure 1. Map of studied Zodarion rubidum populations. Austria: Graz; Czech Republic: Bransouze, Nepomuk, Prague; France: Perpignan, Montpellier, Les Sables; Germany: Berlin, Frankfurt am Main, Mainz, Cologne; Slovakia: Humenné, Nováky, Sereď; Spain: Playa d’Aro.

Table I. List of sites with latitude, average annual temperature, and prosoma lengths of male and female Zodarion rubidum spiders.

| Site            | Latitude (north) | Temperature (°C) | Prosoma mean length±SE (N) |
|-----------------|------------------|------------------|----------------------------|
| Berlin          | 52°30’           | 8.3              | 1.20±0.03 (2) 1.28±0.06 (4) |
| Bransouze       | 49°20’           | 5.0              | 1.16±0.01 (15) 1.23±0.04 (6) |
| Frankfurt am Main| 50°06’          | 9.8              | 1.11±0.01 (22) 1.24±0.02 (21) |
| Graz            | 47°00’           | 9.1              | 1.17±0.02 (22) 1.29±0.02 (27) |
| Humenné        | 48°42’           | 13.0             | 1.23±0.03 (14) 1.40±0.04 (9) |
| Cologne        | 50°00’           | 9.8              | 1.14±0.02 (24) 1.28±0.06 (14) |
| La Playa d’Aro | 41°50’           | 16.2             | 1.27±0.05 (4) 1.47±0.12 (3) |
| Les Sables     | 46°30’           | 9.9              | 1.12±0.08 (3) 1.26±0.07 (3) |
| Mainz          | 50°50’           | 9.9              | 1.28±0.05 (5) 1.36±0.0 (2)  |
| Montpellier    | 43°36’           | 13.7             | –             | 1.43±0.1 (4) |
| Nepomuk         | 49°28’           | 6.3              | 1.21±0.0 (1) 1.31±0.04 (6) |
| Nováky         | 48°45’           | 9.1              | 1.22±0.0 (1) 1.31±0.04 (6) |
| Perpignan      | 42°42’           | 14.7             | 1.29±0.02 (2) 1.45±0.04 (13) |
| Prague         | 50°06’           | 8.9              | 1.21±0.02 (23) 1.33±0.02 (39) |
| Sereď           | 48°15’           | 10.0             | 1.20±0.02 (20) 1.37±0.08 (4) |
Meteorological Centre (Bratislava). For each site of Z. rubidum we used the nearest measure available.

Allometry between lengths of male and female prosoma was studied using reduced major axis regression (RMA) in order to take account of the random variation contained in both male and female samples. In such cases ordinary least-square (Type I) regression is inappropriate for parameter estimation (Fairbairn 1997). A code for RMA was adopted from Kerkhoff and Allen (2002). The effect of two variables, latitude and temperature, on prosoma size of each sex and female/male prosoma size ratio was studied using multiple weighted least-square regression (MWLR). In order to avoid pseudo-replications (i.e. measurements of individuals from the same site in Z. rubidum), mean values were used in MWLR. The number of individuals per site was used as a weight. The minimal adequate model was achieved using a deletion procedure based on the $F$ test (Crawley 2002). Variation in mean prosoma size of males and females were compared using the $F$ test. One population was omitted from analyses that included data on both sexes as it consisted only of females. All analyses were performed within R (R Development Core Team 2004).

**Results**

Regression of the male prosoma size on the female prosoma size, both on the log scale, revealed an allometric relationship (Figure 2). The slope of the linear model was positive (0.889, RMA) while the intercept was negative (−0.069, RMA).

The size of the prosoma in males did not change either with the latitude or with temperature (MWLR, $P>0.14$; Figure 3). In females, the size of the prosoma did not change with latitude (MWLR, $P=0.40$) but increased significantly with temperature (MWLR, $R^2=0.60$, $P=0.0007$; Figure 3).

The variance in prosoma size was 59% larger in females than in males but not significantly different ($F$ test, $P=0.35$). The female/male ratio of Z. rubidum varied between 1.05 and 1.16. It did not change with latitude (MWLR, $P=0.30$) but increased significantly with the gradient of temperature (MWLR, $R^2=0.52$, $P=0.004$; Figure 4).

![Figure 2. Relationship between female prosoma size and male prosoma size (both on the log scale). Linear model was estimated using reduced major axis regression (RMA).](image-url)
Discussion

Our results show that the adult size of *Z. rubidum* spiders decreased with decreasing temperature. A similar pattern has been observed in two web-building species (Benton and Uetz 1986; Piel 1996; Higgins 2000) and many insects (Masaki 1996). Laboratory data, however, provide evidence that spiders respond variably to the change in temperature. In two tiny spiders, *Erigonidium* (Linyphiidae) and *Coliosoma* (Theridiidae), a constant body
size was attained over a wide range of temperatures. In *Misumenops tricuspidatus* (Fabricius) (Thomisidae) body size of adults increased with increasing rearing temperature. But in most spiders of different families, e.g. *Pirata* (Lycosidae), *Neriene* (Linyphiidae), *Neoscona* (Araneidae), higher temperature resulted in maturation at smaller adult body size (Li and Jackson 1996). Thus it appears that different physiological mechanisms determine the body size in spiders.

Observed decrease in body size of *Z. rubidum* was, however, significant only in females. The male size was rather constant over the temperature gradient. This divergent response resulted in size dimorphism cline. The positive slope of the allometric relationship shows that the male and female sizes respond to environmental conditions in the same direction. This result is consistent with many other invertebrate species (Teder and Tammaru 2005). As the slope was less than unity, the female size increases relatively faster than male size. The females are thus more sensitive to environmental conditions than males (Fairbairn 1997). Obviously, the growth of females is more affected by nutritional and environmental stress than the growth of males (Badyaev 2002).

Why are *Z. rubidum* females larger at higher temperature? Females are selected to attain large body size in order to increase their fecundity. Thus at lower temperature they should have lower fecundity. Most optimality models predict that in habitats where growth is faster body size at maturity will evolve to be larger (Atkinson and Sibly 1997). The rate of growth/development is a function of temperature and diet quality as observed in a laboratory study with *M. tricuspidatus* spiders. Li (2002) observed faster development (having fewer molts) at higher temperatures and on an improved diet. Although we have no observation on the rate of development in *Zodarion* spiders under controlled conditions, available data on phenology suggest that their development is faster in warmer habitats. In central Europe *Zodarion* spiders were found to be univoltine (Pekár and Král 2001; Pekár et al. 2005b) while in the Mediterranean they were bivoltine (Pekár et al. 2005a).

A different selecting agent seems to be acting on *Zodarion* spiders than on crickets, where larger body size is attained in univoltine than in bivoltine populations (Masaki 1996). This might be the food quality or quantity that is changing with latitude. Spiders of this genus are exclusive ant-eaters (Pekár 2004). While in the Mediterranean the fauna of ants is dominated by large species (e.g. species of *Cataglyphis*, *Messor*), in central Europe it is dominated by small species (e.g. species of *Lasius*, *Tetramorium*). In central Europe *Z. rubidum* was observed to capture different ants, particularly species of *Lasius* and *Tetramorium* (Pekár 2004). Unfortunately, no data are available on the prey of this species in the Mediterranean. It might be possible that the smaller spider body size is a result of feeding on small ants. The spider might not be able to compensate for smaller prey by higher capture rate as the ants are dangerous and each capture can be fatal to *Zodarion* (S. Pekár, personal observation).

The effect of prey quality is, however, contradicted by the fact that spiders of different sizes were found in habitats in the Czech Republic which have similar ant fauna but differ in temperature (S. Pekár, personal observation). Thus it is rather seasonal prey quantity than quality that affects the size. Prey availability determined by the length of season is in fact confounded with temperature (Chown and Klok 2003). As a result, shorter prey availability in cooler habitats would result in restricted capture and feeding rate. This should have a stronger effect on females than on males which consume less prey. Such explanation was found to be valid in the case of *N. clavipes* (Linnaeus). Females of this species were largest if the growing season was long and prey abundance was high (Higgins 1992, 2000). Similarly, bivoltine *Ctenus* (Ctenidae) spiders were larger in February when
prey biomass was high than in October when prey biomass was low (Gasnier et al. 2002). Thus spiders living in a warm and high-quality environment, where they catch high numbers of prey, can grow relatively quickly and become larger (Vollrath 1980).

It is not clear why males of Z. rubidum maintain a similar growth rate across all the geographical range. It might be also due to different pathways of ontogenic development. Females pass through six while males pass through five instars (Pekár 2000). Canalized higher numbers of instars (Higgins and Rankin 1996) in females leads to a larger body size, which in combination with different prey availability during the last juvenile instar along latitude results in intraspecific variation in female size. A similar observation was made by Higgins (2002) for Nephila spiders. By these means ecological variables influence microevolution of size in males and females within a given species.

It must be stressed that temperature, used as an explanatory variable, was only a proxy measure of a suite of environmental factors in this study. Exact measurements of the temperature from each study site as well as balanced design of sample sizes would have possibly provided better explanation of the relationship. Further field and laboratory studies are thus required to support the observed pattern.

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