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Landscape structure affects activity density, body size and fecundity of *Pardosa* wolf spiders (Araneae: Lycosidae) in winter oilseed rape

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Abstract. In large parts of Europe *Pardosa* spp. (Lycosidae) are among the most abundant wolf spiders in arable fields and potentially important natural control agents of pests. We studied the influence of landscape factors on activity density, adult body size and fecundity of *P. agrestis* in 29 winter oilseed rape fields (*Brassica napus* L.) in Eastern Austria using pitfall traps. Landscape data were obtained for eight circular landscape sections around each field (radii 250–2000 m). Multivariate regression models were used to analyze the data. Activity density was highest when the length of strips of grassy road-sides in the surroundings was highest and distance to the next grassy fallow lowest. Body size was negatively related to activity density and to the length of road-side strips and positively to woody areas in the vicinity of the fields. Clutch size was unrelated to any of the landscape factors tested but was positively correlated with female body size. Woody areas and grassy fallow in the close vicinity of the fields had a positive influence on number of offspring per female and total number of offspring. These results indicate that various non-crop components in the landscape surrounding oilseed rape fields can specifically influence the activity density and fitness-related traits of *P. agrestis* in crops. The possible role of *Pardosa* spp. in natural pest control is discussed.

INTRODUCTION

Agrobiont wolf spiders (Lycosidae) of the genus *Pardosa* are dominant in most arable fields in Central Europe (Samu & Szinetár, 2002; Nyffeler & Sunderland, 2003). As an abundant generalist predator, *P. agrestis* could potentially be a natural control agent of pests (Symondson et al., 2002; Nyffeler & Sunderland, 2003). Recently it was shown by detecting their DNA that *Pardosa* spp. feed on Collembola (Kuusk & Ekbom, 2010) and pollen beetle larvae (Öberg et al., 2011). Therefore, a knowledge of the factors favourable for *Pardosa* species is necessary in order to sustain viable populations that can potentially reduce pest populations.

Arthropod populations in arable fields are characterized by periodic decimation due to agricultural practices followed by a population build-up, mainly due to re-colonization (Wissinger, 1997). Source habitats for spiders re-colonizing arable fields are mainly perennial non-crop habitats that provide refuges during and after disturbances in arable fields (e.g., soil cultivation or harvest) and during winter (Halaj et al., 2000; Pfiffner & Luka, 2000; Geiger et al., 2009). *Pardosa agrestis*' synchronized life-cycle and high dispersal capacity are adapted to these disturbances (Richter, 1970; Kiss & Samu, 2005). Small to medium sized juveniles of *P. agrestis* occur in spring and autumn and are the main colonizing stages as they are able to cover large distances by ballooning (Richter, 1970), while the dispersal ability of larger instars and adults is more limited because of their exclusive cursorial mode of movement.

We hypothesize that the quality, quantity and distribution of non-crop habitats within agricultural landscapes may have a strong influence on the abundance of *P. agrestis* in arable fields because it affects the number of individuals able to colonize fields and their fitness-related traits. Because body size of adult spiders is to a high degree determined by food supply during pre-adult development (e.g., Uetz et al., 2002) and female body size is a major determining factor of fecundity (Beck & Connor, 1992; Kreiter & Wise, 2001) we further hypothesize that *P. agrestis* individuals are larger and females more fecund in complex landscapes that offer more refuges and/or prey than structurally poor landscapes.

To test these hypotheses oilseed rape (OSR) was chosen as the model crop because currently large areas of this crop are planted every year across Europe (1961: 0.61 million ha, 2009: 8.53 million ha; http://faostat.fao.org/site/567/default.aspx). Further, this crop is attacked by a wide range of pest species that may serve as prey for *P. agrestis* (Alford et al., 2003; Zaller et al., 2008b). There is surprisingly little literature on spider ecology in oilseed rape fields (Büchs et al., 1997; Büchs, 2003; Haughton et al., 2003; Jõgar et al., 2004) and to our

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TABLE 1. ANOVA table for final OLS regression models examining the influence of landscape factors on activity density, body size and fecundity of *Pardosa agrestis* derived using stepwise forward selection. Only models containing more than one predictor variable are presented.

Factor	d.f.	Partial SS	*F*	*P*	Partial r^2
Activity density					
Road-side strips (r = 1750 m)	1	1.477	8.4	0.0077	0.187
Distance to fallow	1	0.777	4.4	0.0460	0.098
Full	2	3.298	9.3	0.0009	
Residual	26	4.598			
Body size males					
Road-side strips (r = 1750 m)	1	0.379	20.4	0.0001	0.337
Proportion of fallow (r = 250 m)	1	0.239	12.9	0.0014	0.213
Distance to woody area	1	0.177	9.5	0.0049	0.157
Full	3	0.660	11.9	0.0001	
Residual	25	0.464			
Body size females					
Road-side strips (r = 1500 m)	1	1.010	10.4	0.0036	0.277
Distance to woody area	1	0.472	4.9	0.0373	0.129
Full	2	1.320	6.8	0.0046	
Residual	24	2.332			
Total offspring					
Distance to woody area	1	104,040.66	5.74	0.0241	0.144
Distance to fallow	1	80,782.37	4.46	0.0445	0.112
Full	2	250,413.16	6.91	0.0039	
Residual	26	471,126.15			

knowledge no data exist on how *P. agrestis* in oilseed rape fields is affected by landscape factors.

We investigated the influence of landscape factors on the activity density, body size and fecundity of *P. agrestis* in 29 winter oilseed rape fields located in landscapes of different complexity and composition. We expected that the proportion of non-crop habitats in the surrounding landscape would have a positive influence on this spider and that, due to the species' habitat preferences, open, grass-dominated habitats would be more important than woody areas.

MATERIAL AND METHODS

Study area, OSR fields and spider data

This study was conducted in an agricultural region (ca. 240 km^2) about 40 km east of Vienna, Austria (central coordinates: 16°57′E, 48°04′N). Within this area we studied 29 winter oilseed rape fields embedded in differently structured landscapes ranging from structurally simple to structurally complex. Oilseed rape was sown by farmers in August and September 2004. The study fields were similarly fertilized and treated with herbicides, fungicides and insecticides following common agricultural practice until December 2004 (further details can be found in Zaller et al., 2008a). From January 2005 a 1-ha-area within each study field was not treated with pesticide and used for sampling epigeic spiders using pitfall traps (plastic cups, diameter: 6.5 cm, height: 10.6 cm, filled with 100 ml 4%-formaldehyde solution). In each field three traps were placed along a transect 8 m from the edge of the field (within-transect trap distance: 20 m). The traps were emptied every second week from the end of March until the oilseed rape was harvested at the end of June 2005. In total 114 species of spiders were captured (Drapela et al., 2008), however only adult *P. agrestis* were included in the current study. Pooled activity density for all six sampling dates was used in the data analysis.

Body size was determined by multiplying maximum width of the prosoma by maximum carapace length, measured under a binocular microscope (30 × magnification, ± 0.02 mm), of 10 randomly chosen individuals of each sex at the peak activity density, which occurred 24 May – 23 June 2005. When fewer than 10 males or females were available, all individuals of the respective sex were measured. In two fields no females were caught during the period of peak activity density.

Of the *Pardosa* females captured 87.8 ± 2.7% were *P. agrestis*, therefore, we assumed that the majority of cocoons in the pitfall traps belonged to this species. To assess differences in the fecundity of *Pardosa* females in different fields, cocoons were dissected and larvae and eggs therein counted ("offspring"). Because the number of cocoons per field and total offspring per field were highly correlated (Pearson correlation, $r = 0.984$, $P < 0.001$), only the latter was used in the analysis. Additionally, we calculated offspring per *Pardosa* female and the mean number of offspring per cocoon ("clutch size") for each field.

Statistical analyses

The proportional area of fallow (grassy set-aside fields of different age; see also Moser et al., 2009) and woody areas, and the total length of road-side strips (grassy margins along roads and farm tracks) and hedges in eight circular landscape sectors with radii of 250, 500, 750, 1000, 1250, 1500, 1750, 2000 m surrounding each field were analyzed. Additionally, the distance to the nearest fallow and to the nearest woody area was measured. The calculations of landscape variables were based on a detailed land use map elaborated by field surveys in 2005 using real colour orthophotos (minimum resolution 0.25 m), which were produced using the software packages ArcGIS 9.1 and ArcView GIS 3.3 (ESRI Redlands, CA, USA).

Dependent variables (activity density, mean body size of males and females, total offspring, offspring per female and mean clutch size) were tested for normal distribution (Shapiro-Wilk, $P > 0.05$) and log-transformed if necessary to meet assumptions of ordinary least-squares regression (OLS). We performed a multivariate regression by using a forward stepwise

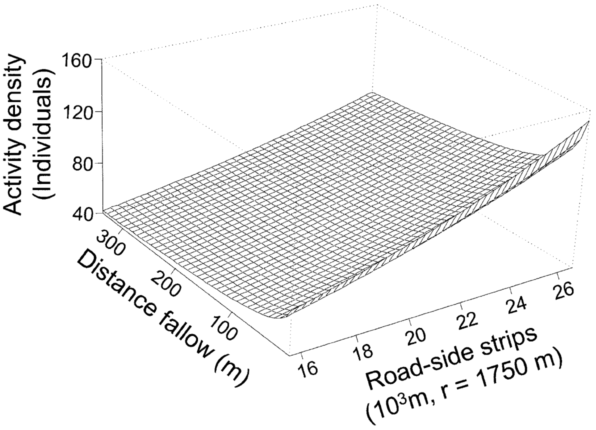

Fig. 1. Relation between activity density of *Pardosa agrestis* and the best explanatory variables (length of road-side strips within a 1750 m radius; distance to next fallow) derived from stepwise multivariate OLS regression analyses.

selection and backward elimination procedure to select the significant predictor variables (Yee & Mitchell, 1991). At each step in the selection of variables the significance of partial effects was tested by dropping each predictor term from the model (Wald test, *F*-statistics, $P < 0.05$; Harrell, 2001). As some landscape variables were correlated (e.g., a landscape variable at different radii and different variables at the same radius), we allowed only the most significant of a group of correlated variables to be included in a multivariate OLS model. The regression analyses were performed with S-PLUS 7.0 for Windows (Insightful Corp., Seattle, USA). Throughout the text measurements and counts are given as mean ± SE.

RESULTS

A total of 2750 *Pardosa agrestis* were captured in the 29 fields studied. Activity density of *P. agrestis* (94.8 ± 11.6 individuals pooled across all fields and six sampling dates) was positively related to length of road-side strips at radius 1750 m and to the distance to the nearest fallow (full model $r^2 = 0.418$, $F_{2,26} = 9.3$, $P < 0.001$; Table 1; Fig. 1).

Mean body sizes of males (5.90 ± 0.01 mm^2; n = 286) and females (7.10 ± 0.03 mm^2; n = 179) were positively

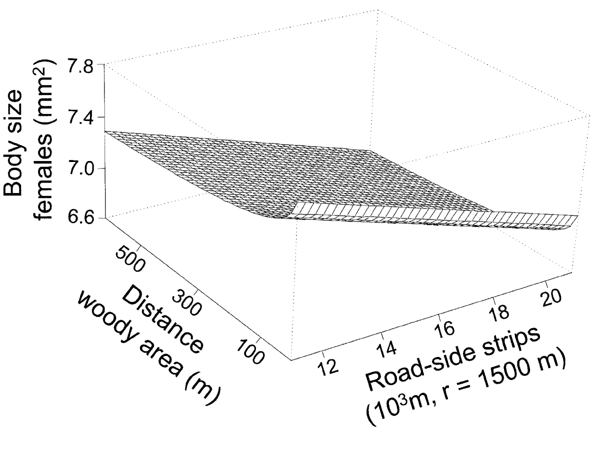

Fig. 2. Relation between mean body size of *Pardosa agrestis* females and the best explanatory variables (length of road-side strips within a 1750 m radius; distance to closest woody area) derived from stepwise multivariate OLS regression analyses.

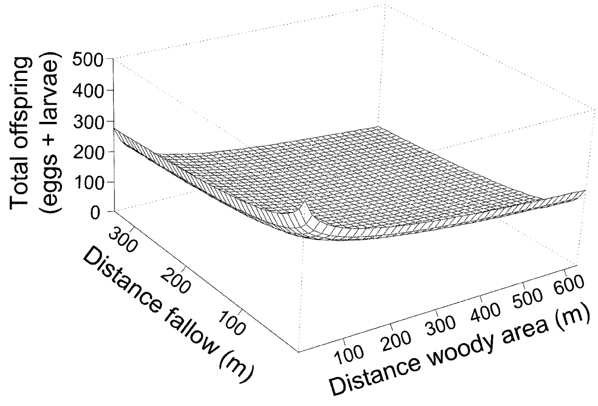

Fig. 3. Relation between total offspring of *Pardosa agrestis* and the best explanatory variables (distance to closest woody area; distance to closest fallow) derived from stepwise multivariate OLS regression analyses.

correlated with each other (Pearson correlation, $r = 0.658$, $P < 0.001$, n = 27). Activity density of *P. agrestis* and mean body sizes of males and females were negatively correlated (males: $r = -0.590$, $P = 0.001$, n = 29; females: $r = -0.397$, $P = 0.040$, n = 27). Landscape variables had similar effects on male and female body size: Length of road-side strips (1750 m radius for males and 1500 m for females) and distance to the nearest woody area were included in both models (Table 1; females: full model $r^2 = 0.361$, $F_{2,24} = 6.8$, $P = 0.005$; Fig. 2). The model for male body size additionally contained proportion of fallow within in a radius 250 m (full model $r^2 = 0.587$, $F_{3,25} = 11.9$, $P < 0.0001$; Table 1).

In total 98 *Pardosa* cocoons collected from 26 fields were included in the analysis. Fecundity measures were differently affected by landscape. The model for total offspring (220.8 ± 29.8 eggs and larvae) contained distance to the nearest woody area and distance to the nearest fallow (full model $r^2 = 0.347$, $F_{2,26} = 6.91$, $P = 0.004$; Table 1; Fig. 3), while offspring per *Pardosa* female (19.2 ± 2.2 eggs and larvae) was best explained by the proportion of woody areas within a radius of 250 m (r^2 =

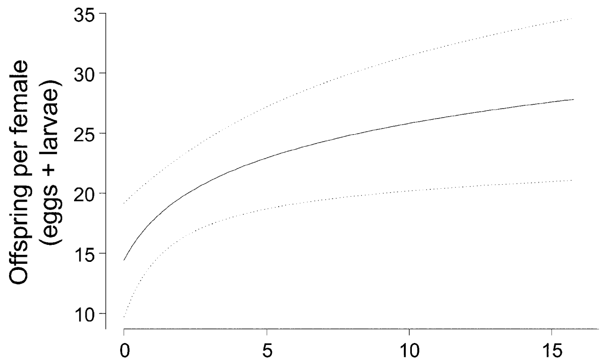

Fig. 4. Relation between offspring number per *Pardosa agrestis* female and the best explanatory variable (proportion of woody areas within a 250 m radius) derived from stepwise multivariate OLS regression analyses (dotted lines show 90% confidence intervals).

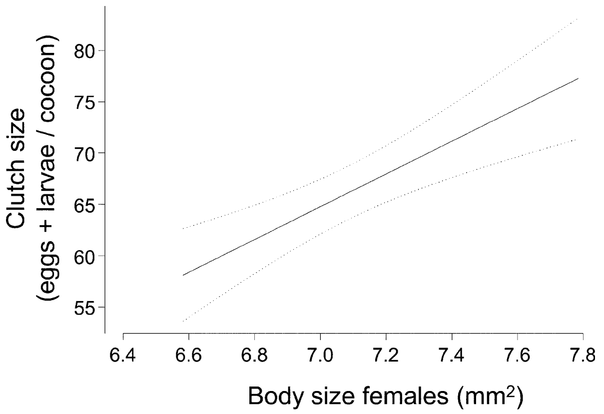

Fig. 5. Relation between mean clutch size (number eggs and larvae per cocoon) and mean body size of *Pardosa agrestis* females (dotted lines show 90% confidence intervals).

0.189, $F_{1,27}$ = 6.3, P = 0.018; Fig. 4). None of the landscape variables was able to contribute significantly to explaining clutch size (65.5 ± 1.9 eggs and larvae). However, clutch size was significantly positively related to the mean body size of *P. agrestis* females (r^2 = 0.364, $F_{1,24}$ = 13.2, P = 0.001; Fig. 5), but not to activity density (r^2 = 0.014, $F_{1,24}$ = 0.344, P = 0.563), total offspring (r = 0.149, P = 0.486, n = 26) or offspring per female (r = 0.378, P = 0.057, n = 26).

Total offspring showed a positive relation to activity density of *P. agrestis* females (r^2 = 0.254, $F_{1,28}$ = 9.2, P = 0.005), which was not the case for offspring per female (r^2 = 0.114, $F_{1,28}$ = 3.5, P = 0.074).

DISCUSSION

The present study demonstrates the importance of different non-crop habitats in the surrounding landscape for activity density and fitness-related traits of *P. agrestis* in oilseed rape fields. *Pardosa agrestis* dominated the spider fauna of the fields studied (24.3 ± 1.8% of the total catch; Drapela et al., 2008) and its activity density was highest when the length of road-side strips in the surrounding landscape was greatest and the distance to fallow was shortest. This finding underlines the importance of surrounding semi-natural non-crop habitats (Hänggi et al., 1995; Halley et al., 1996; Pfiffner & Luka, 2000; Marshall et al., 2006b) for a species of spider that is considered to be mainly dominant in arable fields (Samu & Szinetár, 2002).

The finding that road-side strips within a large radius (1750 m) have a higher explanatory power than fallow in the close surroundings might indicate that the network of road-side strip habitats embedded in the agricultural landscape is facilitating the colonization of arable fields by *P. agrestis* more than patchily distributed fallow. These roadside-strip networks may be more important for the cursorial adult *P. agrestis* than for ballooning young instars (Richter, 1970; Wissinger, 1997). In this respect it is important to note that our study region is generally characterized by relatively small fields (average field size about 1–2 ha) and a rather dense network of roads and farm tracks, which predominantly have 50–100 cm wide vegetated margins. These road-side strips are grassy perennial habitats present throughout the whole study region, while field margins connecting adjoining fields are very scarce. Thus, in the study region road-side strips can be considered to have the same functional role as field margins in other regions. The positive effects of field margins on epigeic arthropods in arable land in general are documented by quite a large number of studies (reviewed in Sunderland & Samu, 2000; Benton et al., 2003; Bianchi et al., 2006), but there is hardly any information on relations at the landscape scale. There are also reports that juvenile spiders respond differently to landscape structure than adult spiders (Bonte et al., 2006), however there is insufficient data to adequately test this. In contrast to our study, Öberg et al. (2008) found no significant positive effect of boundaries in the surrounding landscape on *P. agrestis*. However, these two studies are difficult to compare as the variable "boundaries" calculated by Öberg et al. (2008) includes all boundaries between areas of different types of land-use but only within a 500 m-radius around each field, while the variable "length of road-side strips" used in our study is restricted to road-side strips as mapped by field surveys and was calculated for radii up to 2000 m. A radius of 500 m may be to small to study landscape effects for mobile agrobiont species such as *P. agrestis*, since other studies have demonstrated relationships at greater spatial scales (Schmidt et al., 2008) but no relationships for smaller scales (Öberg et al., 2008; Schmidt et al., 2008).

The explanatory variable that accounts for most of the variability in male and female body size is the proportion of the surrounding landscape made up of road-side strips: the greater the proportion the smaller the spiders. The negative correlations between activity density and mean body size of males and females suggest that density dependent mechanisms might have affected the body size of adult *P. agrestis*. Road-side strips could have enhanced colonization of the fields, which led to stronger intraspecific competition (mainly for limited food resources) analogous to that reported for other species of Lycosidae (Uetz et al., 2002; Balfour et al., 2003). A similar pattern is reported by Öberg (2009), with larger *Pardosa* spiders occurring in structurally simpler landscapes than those in more complex landscapes.

The finding that body size for both sexes was positively related to woody areas in the surrounding landscape might seem surprising because *P. agrestis* is a species of open habitats (Entling et al., 2007). However, in the current study the category woody areas comprised, besides forests and copses, also hedges and shrub land – habitats where *P. agrestis* is recorded in other studies (Hänggi et al., 1995). This indicates that these woody habitats together with associated structures (e.g., forest edges, grassy margins) may be important overwintering sites and refuge habitats providing abundant prey (Pywell et al., 2005; Geiger et al., 2009). Woody habitats in the vicinity may also have indirectly affected *P. agrestis* by altering habitat conditions within the fields (e.g., prey availability). Male body size was additionally negatively related to the proportion of fallow within a radius of 250 m. *Pardosa agrestis* males are known to show high levels of locomotion, especially during the time of reproduction (Samu et al., 2003). Since locomotion is restricted to cursorial movement on the ground at this time and is therefore limited to rather short distances, the influence of fallow was found at the smallest scale. But against our expectations, this relationship was negative. Further studies are needed to reveal the underlying causes.

Total offspring and offspring per female were positively related to woody areas and fallow close to the study fields. Similar to the relations with body size, woody areas and fallow may serve as permanently available habitats or they may improve within-field conditions. Furthermore clutch size was not related to landscape factors but only to female body size and body size was negatively related to activity density, which in turn was enhanced by fallow close to the fields. These relations taken together suggest that population density influenced fecundity indirectly via a decreased size of adult females and consequently smaller clutches (Wise & Wagner, 1992), while the positive effect of non-crop areas in the surrounding landscape was probably due to increased numbers of cocoon carrying females but not due to bigger clutches. The lack of a relationship between landscape structure and *Pardosa* fecundity also accords with the results of Öberg (2009).

Our study highlights important relationships between landscape and spiders, which should be considered when developing natural pest control strategies. Non-crop areas in the surrounding landscape promoted one of the most abundant agrobiont spider species, which accords with other studies on arthropod predators in arable land (Weibull et al., 2003; Clough et al., 2005; Schmidt & Tscharntke, 2005; Schmidt et al., 2005; Schweiger et al., 2005; Isaia et al., 2006; Marshall et al., 2006a; Öberg et al., 2007; Öberg et al., 2008). Since it is not only the type and quantity of non-crop habitats that is important but also their spatial configuration and distribution in the landscape, they should be interspersed within a matrix of arable fields in a way that distances between refuge or source habitats and arable fields are kept short. Our results for *P. agrestis* indicate that relatively small but connecting habitats like road-side strips or field margins become especially important in intensively managed agricultural landscapes. High colonization rates of generalist arthropod predators may be relevant for natural pest control because high predator densities are a prerequisite for pest suppression by generalist predators (Symondson et al., 2002). For oilseed rape, it has been shown that ground-dwelling arthropod predators are able to reduce pest emergence (Büchs & Nuss, 2000; Zaller et al., 2009). Recently, Öberg et al. (2011) showed for the first time that ground-living (*Pardosa* spp.) and foliage-dwelling spiders (*Theridion* spp.) actually consume pollen beetles in the field.

Taken collectively, we found that (i) grass-dominated non-crop habitats were more important for *P. agrestis* activity density than woody habitats but the latter contributed significantly to explaining body size and fecundity; (ii) there is no simple positive relation between body size and non-crop areas; (iii) clutch size was, contrary to total offspring and offspring per female, not affected by landscape factors but only correlated with female body size. To our knowledge this study is the first to address the perhaps underestimated importance of grassy road-side strips for an epigeic arthropod predator at the landscape level. Future research should focus on the role of such networks of perennial habitats in agricultural landscapes for the distribution and dispersal dynamics of epigeic arthropod predators in crop fields.

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