Differences in geographic distribution and habitat of some cryptic species in the *Pardosa lugubris* group (Lycosidae, Araneae) in Belgium

Frederik Hendrickx[1]**, Katrien De Cock**[1]**, Domir De Bakker**[2]
and Jean-Pierre Maelfait[1, 3]

[1] **Department Biology, Laboratory of Animal Ecology**
University of Ghent, K.L. Ledeganckstraat 35, B-9000 Gent
[2] **Department Entomology, Royal Belgian Institute of Natural Sciences**
Vautierstraat 29, B-1040 Brussel
[3] **Institute of Nature Conservation**
Kliniekstraat 25, B-1070 Brussel

ABSTRACT. The habitat and distribution of some closely related species of the *P. lugubris* s.l. group in Belgium are described to contribute to our understanding of the coexistence and speciation of these 'cryptic' species. With a few exceptions, *P. lugubris* has its main distribution in the lower part of Belgium where it occurs on sandy, nutrient poor soils. *P. saltans* occurs widely in Belgium except for in the Campine region where the species is totally absent. *P. alacris* was only found at three localities where limestone outcrops are present. The habitat of *P. lugubris* is pine and birch forests while in *Fagus* woodlands, only *P. saltans* was found. In *Quercus* forests, both species were found, often in mixed populations. A combination of micro- and macroclimatological features and habitat characteristics cause the differences in distribution of these species.

KEY WORDS: *Pardosa lugubris*, habitat, distribution, related species, coexistence.

INTRODUCTION

The lycosid spider formerly described as *Pardosa lugubris* s.l. (Walckenaer, 1802) comprises a complex of different species, of which the taxonomical status has been quite unclear for a long period (WÜNDERLICH, 1984; TÖPFER-HOFMANN & VON HELVERSEN, 1990; KRONESTEDT, 1992; KRONESTEDT, 1999; TÖPFER-HOFMANN et al., 2000). Their almost identical appearance and very similar genital organs are responsible for that unclear taxonomy. The shape and colour pattern of the male palpal cymbium are the most reliable traits to determine the species. Observational studies of the courtship display of the males showed that this behaviour contains the most distinct differences between the species. Such species are often called "cryptic" species. The courtship display is interpreted as the most important species-barrier, as cross species mating tests in the laboratory

revealed that females never accepted a heterospecific male (TÖPFER-HOFMANN & VON HELVERSEN, 1990). At present, six different species of the *P. lugubris* group are formally described: *Pardosa lugubris* s.s. (Walckenaer, 1802), *P. saltans* Töpfer-Hofmann, 2000, *P. alacris* (C.L. Koch, 1833), *P. baerhorum* Kronestedt, 1999, *P. pertinax* von Helversen, 2000 and *P. caucasica* Ovtsharenko, 1979.

Data about the differences in habitat preference and the distribution patterns of these species are still very rare as they were not treated as distinct species in the past. Former records of the habitat preference of *P. lugubris* s.l. in Belgium are light forests and forest edges (ALDERWEIRELDT & MAELFAIT, 1990), and no bimodality or gradient in habitat preference was observed, nor was any heterogeneity found in its distribution. Furthermore, studies that distinguish the different species (DE BAKKER, 1998; TÖPFER-HOFMANN et al., 2000) note that many species live in the same habitat, occupy the same activity pattern and phenology and that combinations of two or even three different species can be found syntopically in mixed populations. This poses the problem of the coexis-

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Corresponding author: F. Hendrickx,
      e-mail: frederick.hendrickx @rug.ac.be

tence and the speciation of these extremely similar species.

Therefore, detailed information about co-occurrence, habitat preference and distribution patterns of the different members of the *P. lugubris* group may reveal if they are "ecologically relevant" species and provide an acceptable explanation for the speciation in the past.

Secondly, we want to investigate which of the different species occur in Belgium. Of the four species in the *Pardosa lugubris* group, only the occurrence of *P. alacris* and *P. lugubris* s.l. has been confirmed until now (ALDERWEIRELDT & MAELFAIT, 1990).

MATERIAL AND METHODS

Geographic distribution patterns

Information about the distribution patterns originated from hand sampling and the results of a research project investigating forest soil arthropod fauna in which 56 different forest plots, evenly distributed over Flanders, were sampled with three pitfalls each during a complete year cycle (see DE BAKKER et al., 1998 for more details), museum collections of the Royal Belgian Institute of Natural Sciences and private collections of M. Janssen, D. Bonte and the first author.

Hand sampling was conducted in the period when adult males are active, from the second half of April till the first half of May in 1999. Because of the unreliability of the determination of the females, males were captured at 20 randomly selected locations (at least 20 males per location). They were kept in alcohol afterwards and determined following Topfer-Hoffman et al, 2000.

The second set of data was obtained from the research project in which 56 different forest plots were sampled. Data from the 25 plots where a species of the *P. lugubris* group was captured were used to analyse the distribution pattern.

Additional data were obtained from re-examination of the material determined as *P. lugubris* s.l. in collections of the Royal Belgian Institute of Natural Sciences and some private collections.

The distribution of each species is presented on a map that shows UTM squares (10 km x 10 km). Maps were created with ArcView version 3.1. Association with soil type was determined by analysing an overlay with a soil map of Flanders.

Habitat characteristics

A description of the habitat was made by estimating the cover (%) of tree, scrub and herb layer. For each layer, the percentage cover of each plant species was estimated in a 10 m x 10 m area encompassing the site where the species were caught. Characterisation of the habitat is based on the composition of the vegetation, the depth of the soil litter layer and the percentage of ground covered by death wood. Data about the habitat characteristics were only available from the above mentioned hand sampling campaign and the research project investigating forest soil arthropod fauna (DE BAKKER, 1998).

A Detrended Correspondence Analysis (DCA) (HILL & GAUGH, 1980) of the vegetation samples was conducted to investigate whether the main factors influencing the composition of the vegetation are also reflected in the occurrence of the different members of the *P. lugubris* group.

To test whether particular plant species are significantly more associated with the occurrence of a certain species, indicator values were calculated for each plant species. Therefore, all vegetation samples were divided into two groups (one for *P. lugubris* and one for *P. saltans*) and the indicator value of each plant species was calculated. Mixed populations were not included in the analyses as we only wanted to specify which plant species are indicative for the habitat of one of the two spider species. As indicator value, we used the IndVal-value (DUFRÊNE & LEGENDRE, 1997), which combines the relative abundance of a species with its relative occurrence in the two groups. To test if a plant species had a significantly larger IndVal for one of the two groups, sites were randomly allocated (1000 times) between the two groups. Significance was evaluated as the rank of the observed value in the randomly generated distribution ordered in decreasing order.

RESULTS

Geographic distribution

In total 100 records about the distribution of the species in Belgium could be obtained. These were divided over 76 UTM squares (20% of all UTM squares of Belgium). Of the six species distinguished in the *P. lugubris* group, only three were found, namely *P. lugubris* s.s. (41 UTM squares), *P. saltans* (44 UTM squares) and *P. alacris* (3 UTM squares). No specimen showed morphological characters that are typical for *P. baerhorum, P. pertinax* or *P. caucasica*. Fig. 1 gives the distributions of the three species over UTM squares. Because the results of the distribution pattern were not related to the method of collection, all data are presented on the same map.

Although there is an overlap in the distribution of the species, some clear patterns can be distinguished. *P. lugubris* has its main distribution in the northern part of Belgium. With a few exceptions, it is almost completely absent south of the rivers Samber and Meuse. The two exceptional records where *P. lugubris* was found south of the rivers Samber and Meuse are both from very warm limestone habitats. The line formed by these two rivers separates the higher parts (200-600 m above sea level) in the south and the lower part (0-200 m above sea level) in the north. In the lower part, it occurs abundantly in the east, called the Campine region. This region is charac-

Clay
Chalkstone
Loam
Limestone + Clay
Schieffer
Sand
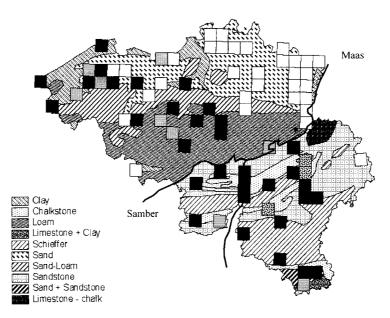Sand-Loam
Sandstone
Sand + Sandstone
Limestone - chalk

Fig. 1. – Overlay of the soil map of Belgium and the map showing 10 km x 10 km UTM-squares where the different members of *Pardosa lugubris* s.l. were found (open UTM squares = *P. lugubris* s.s.; black UTM squares = *P. saltans*; grey UTM squares = *P. lugubris* s.s. + *P. saltans*; dotted UTM squares = *P. saltans* + *P. alacris*)

terised by a relatively continental climate with stronger winters and hotter summers, compared with the western part of Belgium (ALEXANDRE et al., 1992). The soil consists in origin of very nutrient poor and acid sandy soils. An overlay with the main soil types of the northern part of Belgium is plotted on the distribution map in Fig. 1.

In contrast with *P. lugubris*, *P. saltans* appears to be totally absent on the sandy soils of the Campine region in the north-eastern part of Belgium. Its main distribution is located south of the rivers Samber and Maas. North of this line, it can be found on the loamy and sandy loam soils, along the coast, and on the sandy soils in the western part of Flanders.

The third species, *P. alacris* was found to be very rare in Belgium. There were only three locations, all with limestone outcrops originating from the central Devon (south) and the early Carbon (north).
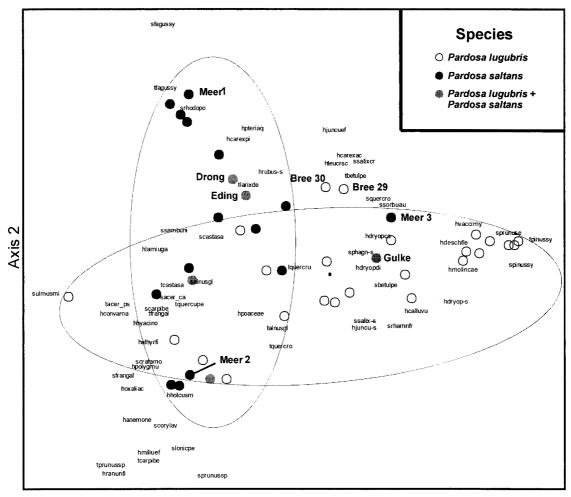
Habitat

No detailed habitat descriptions are available for *P. alacris.* The three known populations occurring in southern Belgium were all found along forest edges on rocky limestone slopes exposed to the south. One of those three populations was mixed with *P. saltans*.

In total 45 plant species lists were available, 24 of *P. lugubris* populations, 16 for *P. saltans* and five for sites in which the two species co-occurred. There were no significant differences (*t*-test; p > 0.05) between the litter depths and the estimated quantities of dead wood for the two species. Localities where *P. lugubris* was captured

showed a much higher cover of mosses, mainly species of the genus *Polytrichium*.

An indirect gradient analysis (DCA) on the basis of the estimated percentage ground cover of the plant species making up the herb (h), scrub (s) and tree (t) layer results in the ordination shown in Fig. 2.

Along the first axis (Eigenvalue: 0.822), *P. lugubris* is present along the whole gradient while *P. saltans* on the other hand is restricted mainly to the left side of the axis. The dominant plant species reveal that this gradient goes (from left to right) from *Fagus*-woodlands and *Quercus* (mainly *Quercus robur*) forests over *Betula pendula* forests to *Pinus sylvestris* woodlands. These forest types indicate that there is a gradient of less nutrient poor, lightly acidic soils (*Quercus robur* and to a lesser extent *Fagus sylvaticus*) towards very acid, nutrient poor sandy soils (*Pinus sylvestris*) (ELLENBERG, 1979; VANDEN-KERKHOVE, 1998; STORTELDER et al., 1999). There are two exceptional populations, indicated in Fig. 2 as "Meer3" and "Gulke" where *P. saltans* was captured in a birch forest. Location "Meer3" was, however, a very small birch forest of only one hectare that is totally enclosed in a large beech and oak forest. Other samples originating from the same forest, indicated as "Meer1" and "Meer2" in Fig. 2, show that they have a vegetation composition which fits well into the *P. saltans* habitat. In the population "Gulke", situated in the western part of Flanders, only a few individuals of *P. saltans* were found amongst individuals of *P. lugubris*. The individuals were captured in a clear-cut area with young shoots of birch trees of only one meter in height.

Fig. 2. – DCA-analysis of the 45 sites based on the vegetation composition. Points represent the presence of *P. lugubris* and/or *P. saltans.* Plant species are abbreviated according to the layer where they were present (h= herb; s = scrub, t = tree) followed by the first five characters of the genus and the first two characters of the species name.

Along the second axis (Eigenvalue: 0.611), *P. saltans* is present along the whole gradient, while *P. lugubris* is restricted to the lower part. Populations on the upper part of the graph were captured in forests where *Fagus sylvaticus* was the dominant tree species, while *Quercus robur* forests are located on the lower part of the axis. Also for *P. lugubris*, there are a few exceptional populations, indicated in Fig. 2. "Bree29" and "Bree30" are from the same forest with a vegetation which was a bit more *P.saltans*-like. This forest is situated in the Campine region in the north-east of Flanders. In "Drong" and "Eding", respectively situated in the loamy sand and the loamy region.

The remaining populations, where both species occur syntopically, are located towards the centre of the ordination of the vegetation samples, where *P. lugubris* as well as *P. saltans* occurs.

Table 1 lists the names of the most encountered plant species (encountered in more than 8% of the investigated sites). They are ordered from highest IndVal for *P. lugubris* towards highest IndVal for *P. saltans*. *Pinus sylvestris* (tree-layer), *Prunus serotina* and *Betula pendula* (scrub-layer) and *Molinia caerulea* (herb-layer) have a significantly larger indicator value for *P. lugubris*. All are indicative for nutrient poor, acid and sandy soils. For *P. saltans*, *Fagus sylvatica* (tree-layer), *Carpinus betulus*, *Cratageus monogyna* and *Fagus sylvatica* (scrub-layer) and *Anemone nemorosa* (herb-layer) have a significantly larger indicator value. Tree species such as *Quercus robur*, *Rubus*-sp. and *Sorbus aucuparia* were encountered at more than 25% of the investigated sites, and showed no higher correlation with one or the other of the two spider habitats.

TABLE 1

List of most abundant plant species ordered from highest IndVal for *P. lugubris* (top) to highest IndVal for *P. saltans* (bottom) (IndVal= Indicator Value following Dufrêne & Legendre, 1997; p-value = level of significance that plant species is indicative for *P. lugubris* or *P. saltans* habitat; total # sites = number of sites where plant species was observed; % of total # sites = total number of sites where the plant species was observed).

Plant species associated with **P. lugubris**				
Species	*IndVal*	*p-value*	*total # sites*	*% of total # sites*
Betula pendula (scrub)	57,35	0,002	13	29
Pinus sylvestris (tree)	45,83	0,001	6	13
Prunus serotina (scrub)	40,5	0,047	11	24
Molinia caerulea (herb)	35,25	0,048	7	16
Sorbus aucuparia (scrub)	30,92	0,326	14	31
Deschampsia flexuosa (herb)	26,99	0,205	8	18
Quercus robur (tree)	26,3	0,635	13	29
Vaccinium myrtilum (herb)	25	0,055	5	11
Plant species associated with **P. saltans**				
Species	*IndVal*	*p-value*	*total # sites*	*% of total # sites*
Fagus sylvatica (tree)	53,22	0,001	8	18
Rubus-sp. (herb)	46,21	0,153	17	38
Fagus sylvatica (scrub)	30,67	0,009	4	9
Anemone nemorosa (herb)	27,37	0,023	5	11
Acer pseudoplatanus (scrub)	26,25	0,137	9	20
Cratageus monogyna (scrub)	25	0,014	4	9
Carpinus betulus (scrub)	25	0,021	4	8
Lonicera periclimenum (srub)	21,67	0,148	4	9
Quercus rubra (tree)	20,57	0,344	6	13
Corylus avellana (scrub)	19,83	0,244	9	20
Pteridium aquilinum (herb)	19,62	0,244	6	13
Hyacinthoides non-scripta (herb)	16,42	0,162	6	13
Betula pendula (tree)	14,62	0,895	8	18

DISCUSSION

Although *P. saltans*, *P. lugubris* and *P. alacris* were sometimes found together in mixed populations, each species, however, seems to have a different optimal habitat, which may explain the difference found in their geographic distribution

The distribution map of *P. lugubris* shows that this species is almost entirely restricted to the sandy soils in the lower part of Belgium. Besides the lower nutrient content of the soil and the vegetation composition, this region is also characterised by a warmer climate during the summer months. This is in part due to the faster warming up of the upper soil layer compared with clay and loamy soils. In the Campine region, located in the eastern part of Flanders, this is even more pronounced because of the lesser cooling influence of the sea (ALEXANDRE et al., 1992). The average temperature south of the rivers Samber and Maas is lower compared to the lower part of Belgium, which could explain the absence of *P. lugubris* in this region. The two exceptional locations where *P.*

lugubris was found south of this line, are characterised by a warm microclimate (ALEXANDRE et al., 1992). Therefore *P. lugubris* seems to be a more thermophilous species than *P. saltans*.

The habitats of *P. lugubris* and *P. saltans* can be divided into three main groups. Firstly, a group where *P. lugubris* occurs alone where typical plant species are *Pinus sylvestris*, *Molinia caerulea*, *Prunus serotina* and *Betula pendula*. Fytosociologically, forests with such a plant composition are assigned to *Vaccinio-Piceetea* (STORTELDER et al., 1999). It is a forest type that is typical for acid and sandy, nutrient poor environments. Most of them are not the original forest type but were planted at the beginning of the 20th century on former heathlands. Forests where *P. lugubris* as *P.saltans* can also be found are mostly dominated by *Quercus robur*, *Quercus petrea*, *Rubus* sp., *Castanea sativa* and *Sorbus aucuparia*. This forest type, called *Quercetea robori-petraeae* (STORTELDER et al., 1999) develops on sandy to sandy loam soils. They are more nutrient rich and less acidic than *Vaccinio-Piceetea* soils (VANDEKERKHOVE, 1998). Sites where *P.*

saltans occurs alone are mainly forests dominated by *Fagus sylvatica*, *Quercus robur*, *Carpinus betulus* and have *Anemone nemorosa* in the undergrowth (*Querco-Fagetea*). This is a quite old forest type, which needs about 100-300 years to develop and has its main distribution on the loamy soils of Belgium. The three records of *P. alacris* seem to indicate that the species is possibly restricted in Belgium to forest edges on limestone.

The results presented here indicate that each of the three represented species of the *P. lugubris* group has its own distinct habitat optimum. A combination of several factors such a micro- and macroclimatological features and habitat characteristics causes the differences in distribution between the different members of the *P. lugubris* group.

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