Life history, habitat use and dispersal of a dune wolf spider (*Pardosa monticola* (Clerck, 1757) Lycosidae, Araneae) in the Flemish coastal dunes (Belgium)

Dries Bonte[1] **and Jean-Pierre Maelfait**[1,2]

[1] **University of Ghent, Dep. Biology, Laboratory for Animal Ecology, Zoogeography and Nature Conservation, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium**
[2] **Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussels, Belgium**

ABSTRACT. *Pardosa monticola* (Araneae, Lycosidae) is a rare spider in Flanders. It is restricted to thermophilic mesotrophic (dune and heath) grasslands. Its life cycle and its habitat preference in the coastal dunes were analysed by interpreting data of more than 200 year-round pitfall-samplings. Viable populations are found in short dune grasslands (grazed by rabbits) and in mown young dune slacks. The life cycle is mixed annual-biannual and hibernation takes place in the juvenile or sub-adult instars. In short grasslands, the species over-winters in the rough neighbouring vegetation, in dune slacks, in litter accumulations. In the latter, the species survives submerging during winter inundation.

Dispersal between suitable habitats can occur by male terrestrial movements via xerophylic habitats and dense grassland vegetation. Aeronautic dispersal is a rare phenomenon in the first instars that takes place only in periods of food shortage. Although a low proportion of the population exhibits this behaviour, this kind of dispersal can be of great importance for gene exchange between distant or strongly isolated populations. The implications and the importance of these data are discussed in relation to contemporary nature management.

KEY WORDS : *Pardosa monticola*, coastal dunes, life history, dispersal, habitat.

INTRODUCTION

In Flanders and in the rest of the Atlantic biogeographical region coastal dunes form a unique biological and geomorphological landscape. Because of the presence of several biotic and abiotic gradients (vegetation succession, sand dynamics, hydrology, lime richness and microclimatological conditions), they represent a high biological diversity in animals and plants (PROVOOST & HOFFMANN, 1996). Contrary to higher plants, the typical arthropod communities are characteristic for sandy and thermophilic habitats such as Marram dunes, grey dunes and short grazed dune-pastures (DESENDER et al., 1991; KOEHLER et al., 1995; BONTE, 1997; BONTE & DE KNIJF, 1997). These habitats are typical of subclimax situations under grazing regimes and/or continuous eolian dynamics (DE RAEVE, 1989).

First of all, the recent expansion of the human population along the coast (tourism) resulted in a significant reduction of the formerly non-urbanised dune surface and hence in a strong fragmentation of the dune entities (VERMEERSCH, 1986). Since fragmentation, sand stabilisation and the retreat of the former agro-pastoral land use enhance vegetation succession to massive dune scrubs and woodland, thermophilic habitats (grey dunes, short grazed dune grasslands) have been strongly isolated on a (sub)regional scale. This fragmentation process is a rather recent phenomenon, which started in the fifties.

Further, predatory arthropods of coastal habitats are probably under constant environmental pressure as a result of the sometimes-extreme climatological conditions and related trophic problems, such as food deprivation from lack of suitable prey under hot, dry circumstances (BONTE et al., 2000a). In addition to this, dynamic eolic processes may destroy potentially optimal habitats. Moreover, fluctuations in grazing intensity by both

domestic and semi-natural grazers (rabbits) may influence vegetation patterns, important for their survival and juvenile development (BONTE et al., 2000a,b).

In addition to the recent habitat fragmentation, these severe climatological conditions and dynamic vegetation processes can result in a high turn-over rate within the arthropod populations, resulting in fairly large amounts of unoccupied but suitable habitat remnants.

There is a general consensus that spiders Araneae are good ecological indicators (MAELFAIT & BAERT, 1988; RUSHTON, 1988; SPEIGHT, 1986; MAELFAIT et al., 1989; MAELFAIT & HENDRICKX, 1998). BLANDIN (1986) defined a special case of bio-indication in which the absence or presence of a species and, in the latter case, its abundance are the bio-indicators. The indicator species concept is, however, problematic because there is no consensus on what the indicator is supposed to indicate (SIMBERLOFF, 1997). In monitoring or habitat evaluation using spiders as indicators, the absence of typical species (stenotopic species) is often indicative for low habitat qualities, i.e. vegetation structure. Whether the absence of the species is the result of the low global ecosystem quality has so far never been questioned. Habitats may be intrinsically suitable but unoccupied due to severe isolation, edge, surface and matrix quality effects.

Although conservation and restoration of thermophilic mesophytic grassland habitats is one of the primordial aims of contemporary (floristically based) dune-management (PROVOOST & HOFFMANN, 1996), the absence of typical arthropod species is generally explained by low habitat quality (MAELFAIT & BAERT, 1996; BONTE et al., 1998) and by the local turnover phenomena (BAERT & DESENDER, 1993; DESENDER, 1996). Whether these factors lead to dynamic, patchily distributed populations is not yet investigated. If so, arthropod populations of these habitats are organised within the several dune-entities as meta-populations. The maintenance of these meta-structured populations is dependant on both the suitability of the habitats and the species-specific dispersal possibilities between the several remnants (HANSKI, 1999). While capture – recapture techniques can be used for butterflies (see e.g. HILL et al., 1996; MOUSSON et al., 1999), they cannot be used for the determination of dispersal of spiders, because of the small size of the juvenile and adult individuals. In order to study spider dispersal, data of pitfall trapping for terrestrial dispersal (BONTE et al., 2000) should be used, while laboratory experiments are necessary for the determination of the species' specific ballooning capability (dispersal via air currents). Ballooning has not been studied thoroughly because of the difficulty of estimating effective dispersal by field- or laboratory experiments (FOELIX, 1996, DUFFEY, 1998). This distant dispersal is probably the determining factor in inter-population exchange of individuals and, consequently, in gene flow.

Within the framework of this study, the distribution, dispersal and life history of the wolf spider *Pardosa mon-*

ticola (Clerck, 1757) have been investigated. This wolf spider is a widespread species in Europe and Asia (ALDERWEIRELDT & MAELFAIT, 1990). In Europe it is typical for short grazed and oligotrophic pastures and heathlands (WIEBES & DEN HOLLANDER, 1974; ALDERWEIRELDT & MAELFAIT, 1990); in the Flemish and Dutch coastal dunes, the species is dominant in rabbit-grazed pastures (VAN DER AART, 1975; MAELFAIT et al., 1989). *Pardosa monticola* is also listed on the Red list of spiders from Flanders (MAELFAIT et al., 1998). Apparently restricted to thermophilic short-grazed dune grasslands, its habitat-binding and multi-habitat use have been studied in order to detect potential migration barriers between the grassland remnants. BONTE et al. (2000a,b) discussed the seasonal migration of several stenotopic grey-dune species and of *Pardosa monticola* via gradient pitfall trapping. The habitat use of *P. monticola* has been studied during the winter-period in both inundating and permanently dry grassland habitats. The data obtained on habitat use, terrestrial migration and hibernation habitat could be used to optimise an 'arthropod-friendly'-dune management.

MATERIAL AND METHOD

Data collection

Habitat use, terrestrial dispersal and life history

From the seventies onwards, spiders have been collected in all possible dune habitats in the Flemish coastal dunes by means of pitfall traps (HUBLÉ, 1975; HUBLÉ, 1976; HUBLÉ & MAELFAIT, 1981; BAERT & DESENDER, 1993; MAELFAIT, 1993; BONTE & HENDRICKX, 1997; BONTE et al., 1999; BONTE, unpub.data; MAELFAIT, unpub. data; VANBIERVLIET, unpub. data). These data from more than 220 pitfalls during more than 30 year-round sampling campaigns, concern more than 130,000 identified adult individuals. Sixty five percent of these traps were placed in dune grasslands, grey and blond dunes.

Within this data-set, we selected all data concerning *Pardosa monticola,* from 61 pitfalls in which the species was present and where data were available on the vegetation composition around the pitfalls. The vegetation composition was studied by means of the 'fast-Londo'-scale, so only the coverage of the dominant plant species was taken into account in the analysis.

Although population densities can undergo year-to-year fluctuations (BAERT & DESENDER, 1993), we assume that a total analysis of these data in relation to the different habitat types results in a good description of the habitat of adult *Pardosa monticola* by comparing total annual catches between the discerned habitats. Apart from the total abundance, we also investigated the differences in the ratio of males/females between the different habitats. A dominant male activity registered from the pitfalls indicates a higher abundance of the latter. While juvenile terrestrial activity is a patchily restricted phenomenon

related to feeding and searching for suitable hibernation habitats (BONTE et al, 2000b), male activity can be interpreted as the only terrestrial activity developed outside the native population in searching for suitable mating partners in other suitable habitat patches (MAELFAIT & BAERT, 1975).

In addition to this data collection, a quadrat sampling (30x30 cm²) was performed to estimate winter densities in a mesophytic dune grassland and a young dune slack in De Panne during 1995-1997. Thirty replicas were taken in respectively the short grazed grassland; the rough grassland border and the litter beneath *Salix repens*-shrubs, the young dune slack before and after a long winter inundation. Periodic hand collection was carried out in the mesophytic grassland of the Westhoek-reserve in De Panne in order to reconstruct the life cycle from field data by measurement of the cephalothorax width of juveniles and adult individuals with a measurement ocular (cf. TOFT, 1976).

Laboratory experiment for aeronautic behaviour

Spider dispersal occurs not only via terrestrial migration: an even more important way for distant migration in spiders is aeronautic dispersal (DECAE, 1987, FOELIX, 1996). In order to estimate the proportion of potential aeronauts in *P. monticola,* we conducted laboratory experiments in a test chamber as designed by LEGEL & VAN WINGERDEN (1980). The temperature within the test chamber was 30°C, the wind velocity 0.25 m/s and the relative air humidity was 40%. Individuals displaying tiptoe-behaviour (i.e. stretching of the legs, followed by rising the abdomen and the production of silk threads) were considered to be ready for aeronautic behaviour. Juveniles from five females with cocoons from three different populations (two in the Westhoek-reserve, De Panne, and one from Ter Yde, Oostduinkerke) were reared under standard laboratory conditions (20°C, ±60 % RH). The juveniles were fed with eight *Drosophila* flies per week. After each moult, the individuals were tested in a well-fed condition (8 flies/week) and a starving condition (no prey for one week). Since the total number of females per sampling place was too small to analyse differences within populations, data from the three populations were pooled in this preliminary assessment of the ballooning capacity.

Data analysis

The reconstruction of the life history of *P. monticola* (seasonal growth) was performed by measuring the cephalothorax width of the caught juvenile and adult individuals from one dune grassland. When these measures are plotted against the period in which they were caught, the life-history pattern becomes visible (TOFT, 1976). Since the measurements of the cephalothorax overlap, it is difficult to disentangle the different juvenile instars or the adult cohorts. The latter can be deduced by the analyses of the frequency diagram, based on the cephalothorax measurements of the adult individuals. Since the different cohorts are visible in different unimodal distributions (SEGERS, 1989; SEGERS & MAELFAIT, 1990, BONTE & MAELFAIT, 1998), the different distributions were disentangled by the application of the program Mixture 1.0 (VAN DONGEN et al., 1999), which was originally designed for the analysis of Fluctuating Asymmetry data. Different models (combinations of different normal – unimodal-distributions) can be tested against each other by the application of a bootstrapping procedure. These data enabled us to reconstruct the expected summated distribution, via z-statistics, which were compared with the observed frequencies by χ^2-goodness of fit tests (JERROLD, 1996).

By using Euclidean similarity dendrograms and non-metric multi-dimensional scaling ordination (MDS: KRUSKAL & WISH, 1978) we were able to classify the pitfall data into several habitat-groups and hence to study the different determining vegetation characteristics. Multivariate analysis by applying MDS enables us to study non-linearly or non-normally distributed biological data. Because the ordination is based on different iteration algorithms, both a stress-factor and a significance level are listed. The stress is a measure of deviation from monotonicallity and the dissimilarity (distances) in the original and reduced ordination. A high stress-factor indicates an ambiguous ordination, a low one represents an ordination that is a good reflection of reality (CLARCKE & AINSWORTH, 1993).

An important advantage of this methodology is the possibility to calculate a stress-factor (an indication of the ordination stability) and hence the ordination significance via a randomised Monte-Carlo permutation test.

Plant species composition, spider abundance and sex-ratio differences within the clustered habitat types were analysed by one-way ANOVAs and Scheffé post hoc tests.

Independent t-tests were used for the analysis of quadrat densities between the different hibernation habitats. Both differences in occupancy between the several habitat classes and ballooning proportions between the tested different instars and the feeding regimes were analysed by applying sequential Chi-square tests for the comparison of proportions. Bonferroni corrections were used for the elimination of multiple testing errors. The different analyses were performed with the Statistica 5.0, Primer 3.1 and the PC-ord 3.03 software.

RESULTS

Life cycle

The life cycle of *Pardosa monticola* can be derived from Fig. 1. In the Flemish coastal dunes, adulthood is reached in the period May-June, which is also the mating season. Shortly after, the males die. Females live till September and from June till August-September, they
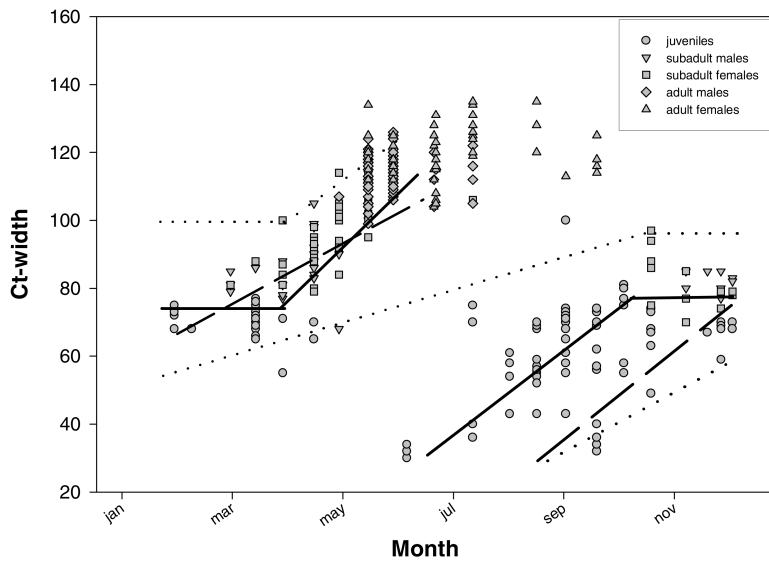
Fig. 1. – Seasonal growth of *Pardosa monticola* in a dune grassland in the Flemish coastal dunes (Full line: cohort I; long dashed line: cohort IIa; dotted line: cohort IIb).
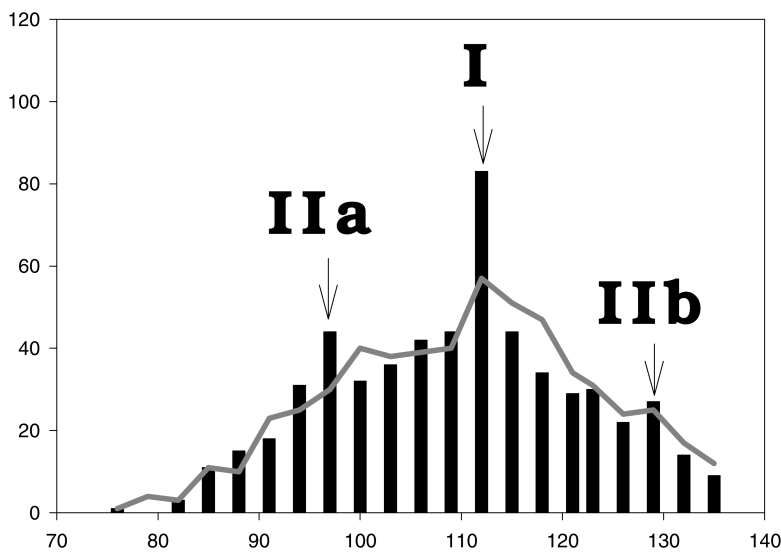

Fig. 2. – Cephalothorax width frequency diagram (bars) with the expected summated normal distribution (Red line).

produce several broods (two?). This results in two periods with early juvenile instars: June-July and September. Juveniles of the first brood hibernate as large juveniles and as sub-adults, as opposed to those of the second brood, which hibernate as smaller juveniles. This life cycle pattern results in two or three cohorts, which can be deduced from the cephalothorax width diagram from adult males measurements (Fig. 2): the trimodal distribution is characterised by the lowest log-likelihood (Table 1) and is significantly different from a bi- and unimodal distribution (Bootstrapping, 100 permutations, p<0.05). The hypothesis that the calculated estimated distribution does not fit the observed pattern should be accepted for the unimodal ($\chi^2_{0.05,20} = 31.41$; $\chi^2 = 212.93$; χ^2-goodness of fit-test) and the bimodal model ($\chi^2_{0.05,20} = 31.41$; $\chi^2 = 75.57$, χ^2-goodness of fit-test). The trimodal distribution should be accepted at the 0.05-level ($\chi^2_{0.01,20} = 37.65$; $\chi^2 = 36.68$, χ^2-goodness of fit-test). The hypothesis should, however, been rejected at 0.01-level because of a higher number of observations at the distribution means in comparison with the expected model (Fig. 2).

As a result, the adult population of *P. monticola* can be divided into three cohorts with proportions of 48.8% of cohort I, 38.8% of cohort IIa and 12.3% of cohort IIb. So, the first-brood spiders will reach adulthood in the next spring (annual life cycle: cohort I). The majority of the individuals of the second brood will also reach adulthood in one year (cohort IIa), while a minor part will become mature after one more hibernation (cohort IIb);

TABLE 1

Results of the mixture-analysis for the separation of different mixed unimodal distributions within the cephalothorax-width frequency data (567 measurements)

Tested model	Normal distribution number	Mean cephalothorax width of the different distributions	Variance	Proportion of the data-set belonging to the distribution	Log-likelihood
Unimodal	1	111.16	18.77	1.000	-1638.95
Bimodal	1	97.10	7.85	0.372	-1630.49
	2	118.57	9.98	0.628	
Trimodal	1	97.03	7.23	0.388	-1623.77
	2	111.78	5.44	0.488	
	3	130.75	1.85	0.123	

they will overwinter a second time and become adult in their second spring (biannual life cycle). This differentiation in seasonal growth is reflected in the cephalothorax-width variation of the adult spiders.

Habitat use, terrestrial and aerial dispersal

Habitat preference of the adult P. monticola

The similarity dendrogram indicates the presence of *Pardosa monticola* in six different habitat types (Fig. 3): grey dunes, blond dunes, shrub edges, tall grasslands (both wet and dry), short grasslands and young dune slacks. Each type is characterised by a typical floristic composition (Table 2). The grey dunes are characterised by a moderate coverage of bare sand and open mosses (mainly *Tortula ruralis ruraliformis*) and the blond dunes by a high amount of bare sand and *Ammophila arenaria*. Shrub species (*Hippophae rhamnoides, Ligustrum vulgare, Salix repens*) and *Calamagrostis epigejos* are typical for the stations situated along the shrub borders. *Avenula pubescens* is abundant in the two mesophilic grasslands. The rabbit-grazed pastures are covered with typically mesophylic herbs (*Galium verum, Helianthemum nummularium, Potentilla neumanniana* and *Thymus pulegioides*) and open mosses (mainly *Hypnum cupressiforme*). The tall grasslands on the other hand are characterised by a dense sward consisting of *Calamagrostis epigejos, Arrhenaterium elatius* and *Rosa pimpinellifolia*. Finally a large amount of bare sand and the presence of freatic plant species (*Carex trinervis, C. flacca* and *Salix repens*) are typical for the young dune slack. The sampling stations situated in the young dune slacks are characterised by nearly annual inundations, because of their low height above the freatic water-level. The other habitats are typically xerophilic (SCHAMINÉE et al., 1996).

The syntaxonomical classification according to SCHAMINÉE et al. (1995, 1996, 1997) is listed in Table 2.

The MDS-ordination confirms this dendrogram clustering (Fig. 4). The stress-factor is moderate (0.129) and the ordination in two axes is significantly stable (Monte Carlo-permutation test: 99 runs; p=0.01). Pearson correlation results of the vegetation characteristics with the two axes are listed in Table 3. The differentiation along the first axis can be interpreted as the variation in moss and herb coverage. The second axis represents the gradient from open, bare sandy habitats to well-vegetated habitats.

In proportion to the total number of analysed traps within a habitat type, the amount of occupied traps is significantly higher in the short grasslands and the young dune slacks (χ^2-test; p<0.001; χ^2=12.94) than in the shrub edges, tall grasslands and blond dunes. A pair-wise comparison of the occupancy proportion did not reveal any differences between these groups (χ^2-test; χ^2<3.00; p>0.05). This indicates a higher occupancy rate in short grasslands and dune slacks.
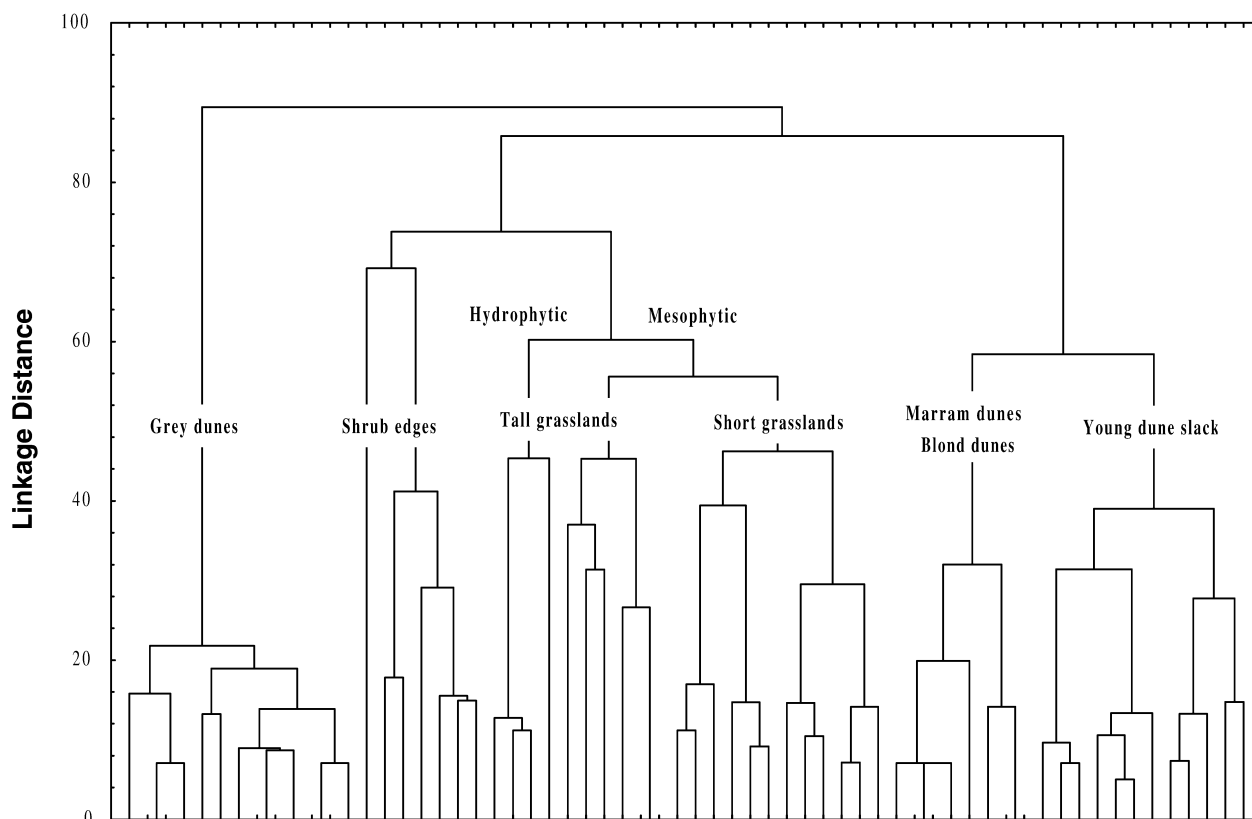

Fig 3. – Bray Curtis similarity dendrogram of the vegetation composition around the pitfall traps with *P. monticola*.

TABLE 2

Plant species composition, vegetation typology, number of traps of the distinct habitat types of *Pardosa monticola* in the Flemish coastal dunes. Marked coverages per plant species (incl. coverage bare sand and non overgrown -open- moss) do not differ between the respective habitats (one way ANOVA, post hoc Scheffé-test, p>0.01)

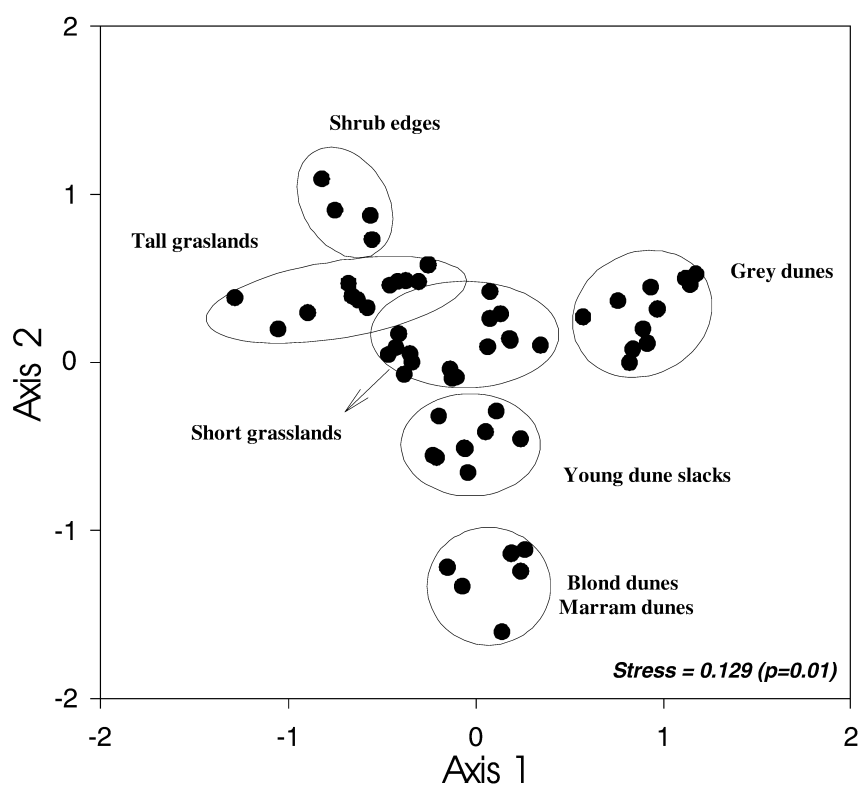|	Grey dunes	Shrub edges	Tall grassland	Short grassland	Blond dunes	Young dune slack
Vegetation typology (Schamminée et al., 1995, 1996 & 1997)	*Tortulo-Koelerion*	*Trifolio-Geranietea sanguinei*	*Arrhenatheretum elatioris*	*Polygalo-Koelerion*	*Ammophilion arenariae*	*Parnassio-Juncetumatri-capillia*
Total number of traps in type	28	28	36	24	35	15
Total number of traps with *P. monticola*	10	7	9	18	6	12
Mean coverage:						
Bare sand	15.76	2.4	0	5.41	80.5	37.72
Open moss	77.15	12.14	13.5	28.75	5.75	10.9
Ammophila arenaria	0	0	0	0	10	0
Arrhenaterium elatius	0	15.71	10	0	0	2.72
Avenula pubescens	0	7.85	38	23.75	0	1.36
Calamagrostis epigejos	0	36.42	15	0	1	4.54
Carex arenaria	3.23**	1.75**	0.6*	7.08	0	2.45***
Carex flacca	0	0	0	1.35	0	15.72
Carex trinervis	0	0	1.5	0.08	1.75	9.54
Festuca rubra	1.53	0	1.4	5.41	0.75	0
Galium verum	0	0.71	5.5	9.16	0	0
Helianthemum nummelarium	0	0	0	7.08	0	0
Hippophae rhamnoides	0	33.14	0.5	0	0	3.63
Ligustrum vulgare	0	10	0	0	0	0
Poa pratensis	1.15*	2.14*	2.5*	8.75	0	0.45
Potentila neumanniana	0	0	0	7.5	0	0
Potentila reptans	0	0	0	2.08	0	0
Rosa pimpinellifolia	0	0	18	0	0	0
Salix repens	0	20.71	5.5	0.16	1	11.18
Thymus pulegioides	0	0	1	1.2	0	0

Fig. 4. – MDS-ordination of the pitfall traps containing *P. monticola*, based on the vegetation composition. Typology cfr. Bray-Curtis analysis (Fig. 2, Table 1).

TABLE 3

Pearson correlations of the identified plant species (incl. coverage bare sand and non overgrown –open-moss) with the two axes of the MDS-ordination

	Axis 1		Axis 2	
Coverage of:	r	p	r	p
Bare sand	0.218	0.09	-0.939	**< 0.001**
Open moss	**0.846**	**< 0.001**	**0.367**	**0.004**
Ammophila arenaria	-0.053	0.685	**-0.465**	**< 0.001**
Arrhenatherium elatius	**-0.513**	**< 0.001**	**0.389**	**0.002**
Avenula pubescens	**-0.685**	**< 0.001**	**0.339**	**0.007**
Calamagrostis epigejos	**0.570**	**< 0.001**	**0.467**	**< 0.001**
Carex arenaria	0.210	0.104	0.228	0.077
Carex flacca	-0.040	0.760	-0.179	0.166
Carex trinervis	-0.073	0.574	-0.172	0.183
Festuca rubra	0.125	0.337	0.116	0.372
Galium verum	**-0.398**	**0.001**	0.193	0.136
Helianthemum nummelarium	-0.148	0.255	-0.002	0.986
Hippophae rhamnoides	**-0.366**	**0.004**	**0.390**	**0.002**
Ligustrum vulgare	-0.023	0.857	0.126	0.331
Poa pratensis	-0.141	0.276	0.286	0.025
Potentila neumanniana	0.030	0.816	0.075	0.562
Potentila reptans	0.089	0.493	0.043	0.737
Rosa pimpinellifolia	-0.229	0.075	0.216	0.094
Salix repens	**-0.415**	**0.001**	0.243	0.059
Thymus pulegioides	-0.082	0.526	0.178	0170

The superpositioning of the total number of individuals caught per pitfall (Fig. 5) visualises the dominant abundance of the species in the short-grazed dune grasslands and in the young dune slacks. This observation is confirmed by the one-way ANOVA-analysis ($F_{1,5}$ = 6.94; p<0.001: Table 4): annual abundances are significantly (Post-hoc Scheffé-test, p<0.01) larger in these habitat types. The numbers do not differ between the other occupied habitats (grey dunes, tall grasslands, shrub edges and blond dunes; Post-hoc Scheffé-test, p>0.01).

TABLE 4

Mean abundance and sex-ration per pitfall trap within the six distinguished habitat types. Same letter codes in the 'Post-hoc difference' column indicate no significant difference (Post-hoc Scheffé-tests, p>0.01)

Habitat type	Post-hoc difference	Mean abundance *P. monticola* /trap	Mean sex-ration females: males/trap
Blond dunes	A	1.256	0.000
Tall grassland	A	23.000	0.132
Young dune slack	B	96.583	0.385
Short grassland	B	10.917	0.361
Grey dunes	A	13.384	0.118
Shrub edges	A	3.421	0.000

Sex-ratio in the different occupied habitats

The sex-ratio differences within *P. monticola* between the different habitats show an analogue pattern for the species abundance. The proportion mm/ff are plotted on the MDS-ordination in Fig. 5 (sex-rations > 10 are plotted as equal values). Since the proportion ff/mm is well correlated with the total numbers per trap (Pearson correlation, r=0.72; p<0.001), habitats sharing a low abundance are characterised by a high proportion of males. This observation is confirmed by the variance analysis of this proportion between the different habitat types (one-way ANOVA, $F_{1,5}$=14,63, p<0.001). Post hoc Scheffé-tests reveal significant differences (p<0.01) between young dune slacks, short grasslands and the other occupied habitats (Table 4). The higher proportion of males in the marginal habitats suggests male dispersal via these habitats without the establishment of viable populations.

Hibernation in rabbit-grazed dune pastures and young dune slacks (Table 5)

Density estimates during the winter in both short vegetation (rabbit-grazed pasture and mown dune slack) and in higher vegetation reveal a significant difference between the rabbit-grazed and the rough dune grassland (independent t-test, p<0.001). In the dune slack however, mean densities do not differ between the mown and unmown vegetation. Although the mown parts were inundated dur-
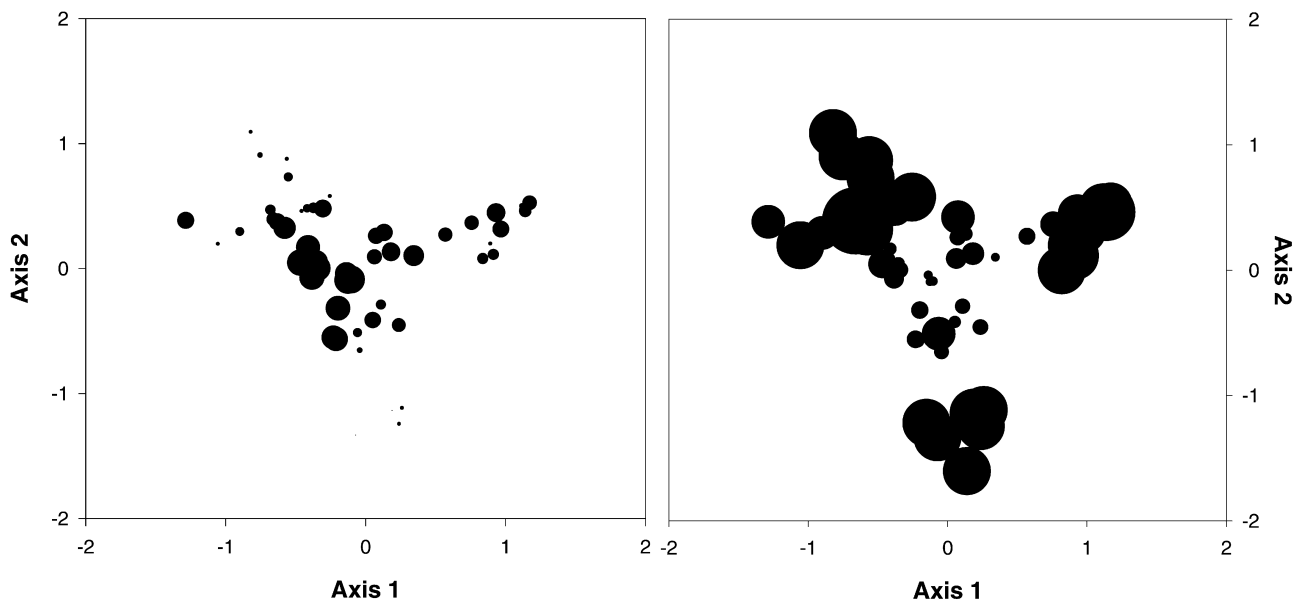
Fig. 5. – Superpositioning of the abundance (left) and sex-ratio proportion males:females (right) on the MDS-plot (Fig. 3).

TABLE 5

Mean densities and 95% confidence intervals of overwintering *Pardosa monticola*, based on 30 replica's of 30x30 cm^2 in different vegetation in a mesophytic grassland and an young dune slack. Densities in vegetation marked with * are significantly different (dependent t-test, p<0.001)

Habitat	Vegetation	Mean density	Conf. int.
Mesophytic grassland:	Tall vegetation (border)*	0.56	0.27
	Short vegetation *	0.00	0.00
Young dune slack:	Litter under Salix repens	0.40	0.17
	Slack: litter before inundation	0.56	0.23
	Slack: litter after inundation	0.46	0.17

ing two months, the mean densities remained the same before and after the inundation (independent t-test, p>0.05). Since no individuals were trapped in pitfalls during this period, we may conclude that *P. monticola* stayed in the inundated litter and did not move to higher and dry habitats.

Aerial behaviour under laboratory conditions

Aerial behaviour of spiderlings of *P. monticola* was only observed in the second, third and fourth instar (Table 6). When the spiderlings were well fed with *D. melanogaster*, no tiptoe behaviour was observed. However, when starved, tiptoe behaviour was shown in 7.1 % of instar II and in 10.5 % of instar III of the tested individuals. This proportion was significantly higher than in the well-fed individuals (instar II: dependent χ^2-test; χ^2=6.33; p<0.05; instar III: dependent χ^2-test; χ^2=4.14; p<0.05). In general, the proportions of ballooning spiderlings within instar II and III did not show any differences (χ^2-test; χ^2=3.02, p=0.22).

TABLE 6

Total tested and ballooning individuals per instar after one week starving

Instar	Total tested individuals	Total individuals showing tiptoe behaviour
II	64	4
III	59	6
IV	45	0
V	38	0

This means that under food shortage, the proportion of potential aeronauts (based on the population structure in the field – proportion in instar X * proportion of potential aeronauts in instar X) reaches peaks in July (1.25-4.15 %) and August-September (0-1.47 %) (Table 7). Using the data of RICHTER (1970), this proportion increases to 12.07±5.82 % in July, to 3.54±1.71 % in August and to 5.95±2.87% in September.

TABLE 7

Estimated proportion of aeronautic juveniles in a general *Pardosa monticola* population of the Flemish coastal dunes

Instar-month	Proportion potential aeronauts in the population	Estimated proportion (%) of aeronauts (this study)	Estimated proportion (%) of aeronauts (data Richter, 1970)
I-6	0	0	0
II-6	0	0	0
I-7	0.45	4.14	12.07±5.82
II-7	0.2	1.28	5.31±2.56
I-8	0.13	0.81	3.54±1.71
II-8	0.13	0.53	3.54±1.71
I-9	0.22	1.47	5.95±2.87
II-9	0	0	0
I-10	0	0	0
II-10	0	0	0

DISCUSSION

Although only based on measurements from one population, the mixed annual-biannual life cycle of *Pardosa monticola* that we observed seems to be typical for the genus *Pardosa* species in NW-Europe (DEN HOLLANDER, 1971; ALDERWEIRELDT & MAELFAIT, 1988; SEGERS, 1989; BONTE & MAELFAIT, 1998). In general, adult spiders of *P. monticola* are present from May till October. Mating takes place in May-June and the adult males disappear from the population in July. Females with cocoons are present from June till the end of September; this is also the period during which spiderlings hatch. The greater amount of observations than expected around the mean of the observed cephalothorax-width measurements probably indicates a rather synchronised hatching period in June and in the late summer. If the hatching period was continuous during the summer, the cephalothorax width of the adult males would have been characterised by a higher amount of variance around the mean instead of the observed leptokurtic distribution. A consequence of this life cycle pattern is the hibernation of the species in a juvenile life-stage.

Large populations with both males and females are present in two habitat types: short grazed dune grasslands and young dune slacks with a low sedge (*Carex flacca* and *C. trinervis*) and Creeping willow (*Salix repens*) vegetation. Our data suggest that the species does not hibernate in open grassland situations, but in the litter of the shrub layer, where winter temperatures are less extreme (DE BACKER, 1963, BARKMAN & STOUTJESDIJK, 1987). The winter-density estimates confirm these findings, since quadrat densities of juveniles are significantly larger in the shrub litter than in the rabbit-grazed pastures. In the young dune slacks, however, hibernation takes places in the *Salix repens* litter, which is still present as a result of the late mowing regime for the conservation of late-summer flowering plants such as *Parnassia palustris*. Although no data are present about the species' cold

resistance, KIRCHNER (1973) found that the supercooling points of species with analogue habitat preferences were intrinsically comparable, and for grassland species lie between –10°C and –4°C during the winter period. The temperature in short grazed dune-pasture grasslands will decrease to –5°C during severe frost (air temperature of –5.4), while the temperature in the litter will never be less than –0.8°C (ANTHEUNIS, 1969 and BONTE, unpub.data). As a consequence these 'thermophile' habitats are unsuitable for the species' survival during the winter period. Analogue multi-habitat use has also been demonstrated by EDGAR (1970: *Pardosa lugubris*; Araneae), DENNIS et al. (1994: *Tachyporus hypnorum*; Coleoptera, Staphylinidae and *Demetrias atricapillus*; Coleoptera, Carabidae), DELETTRE et al. (1998: Diptera, Empidoidea) and BONTE et al. (2000a): *Typhochrestus digitatus, Pelecopsis nemoralis*: Araneae) in grass- and woodlands.

Apparently the species is able to withstand long periods of winter inundations since densities are hardly affected after the inundation period. The species' inundation tolerance is remarkable and may also explain its presence in saltmarshes around Mont Saint Michel (France; FOUILLET, 1988). In our country *Pardosa monticola* is absent from this habitat but replaced by its sister-species *P. purbeckensis* (ALDERWEIRELDT & MAELFAIT, 1990; HENDRICKX & MAELFAIT, 1998), which is also characterised by a high inundation tolerance resulting from the presence of hydrophobic hairs on its abdomen. As opposed to the latter, however, *P. monticola* is generally a species typical of dry habitats. Although the spiders' population densities are not affected by winter inundations (in contrast to different butterfly species: LEJEUNE et al., 1955; BERRY et al., 1996 and other spider species: DECLEER 1988), submerging of the habitat during the winter can have a marked impact on the species long-term survival and fitness (JOY & PULLIN, 1997): it will significantly decrease the population's viability. These long-term effects should consequently be studied in order to estimate the global effects of the winter inundation.

In the adult stage, *Pardosa monticola* migrates only via terrestrial movement. Terrestrial migration may occur in two ways: dispersal for the colonisation of new habitat remnants and seasonal dispersal between the hibernation sites and the adult mating and feeding habitat, as discussed above. Our study indicates that mainly male individuals leave their optimal reproduction habitats for the foundation of other suitable habitat remnants. This terrestrial dispersal seems only to occur via open xerophylic habitats (grey and blond dunes) and higher grassland or dwarf-shrub vegetation (*Arrhenatheretum elatioris* grasslands, with or without *Rosa pimpinellifola* dwarf shrubs). The catches in shrub borders may indicate both dispersal along shrub edges and withdrawal into this habitat-type for hibernation.

In contrast to some other Lycosid species (GREENSTONE et al., 1985, MILLER , 1984; BLANDENIER & FÜRST, 1998; BONTE et al, 1998; DUFFEY, 1998), aerial dispersal of *Pardosa monticola* in the field has never been described. Our laboratory experiments, however, indicate that a small proportion of the population does show pre-ballooning behaviour. In comparison with the results of RICHTER (1970) (ballooning proportions of 26.55 ± 12.81 % of species of the second instar - cephalothorax length of 0.8-1 mm), our study showed a low proportion of ballooning individuals. This may indicate that aerial dispersal differs from population to population and has as a consequence been submitted to natural selection. (SUTCLIFFE et al., 1997; HILL et al., 1999). We should, however, be careful in making the comparison because it is not known whether the testing conditions are similar in both studies: temperature and air humidity in both the testing chambers were the same, but nothing is known about Richter's feeding and breeding conditions during the experiment.

As RICHTER (1970) and GREENSTONE et al. *(*1985) discussed, only the first instars are able to balloon due to their low body mass. In our experiment however, the species only showed tiptoe-behaviour when they were starved. This is in agreement with the findings of VAN WINGERDEN (1980a, b) and WEYMAN & JEPON (1994) who investigated Erigonid spiders in the laboratory and in field situations and observed higher take-off rates when food was deprived. In our case this means that the species will probably only disperse via ballooning when food availability is limited as a result of meteorological conditions or high densities of other predators. The food of the early instars mostly consists of larger Collembola of the genus *Entomobria* and *Isotoma*. In dry and hot weather conditions, these species will migrate into the soil (into the F-layer, which consists of fragmented plant material) and become unavailable for the predator (BONTE & VAN EUVERSWYN, unpub. data). Since these meteorological conditions, which in turn enhance aerial dispersal (VUGHTS & VAN WINGERDEN, 1976), occur during the juvenile period (BONTE et al., 1998), ballooning is probably a regularly occurring phenomenon. This hypothesis, however, needs further field research.

As stated by THOMAS (1996), aerial migration is only effective over relatively short distances (up to 3.5-4 km), while terrestrial dispersal is effective on an even smaller scale. These findings would imply that the species should easily be capable of moving between suitable habitat remnants in 'open' dune landscapes via male wandering. Cursorial dispersal via male movement in shrubby dune landscapes is impossible because of the unsuitable migration matrix. On a small scale, however, exchange of individuals between isolated populations should be possible via ballooning. The chance, however, of effective exchange of individuals within these metapopulations will depend on (1) the distance and the patch surface, determining the chance of colonisation and (2) the intrinsic dispersal rate of the source population (influenced by external stimuli such as food deprivation - possibly as a consequence of population densities and weather conditions), which may differ between different populations.

Exchange of individuals between distant populations from remote dune entities, separated by unsuitable urbanised or polder areas, is probably impossible. As a consequence gene flow between fragmented dune entities is inhibited and probably only occurs within the metapopulations from one dune entity.

Implications for conservation

Since the presence of *P. monticola* is affected by the presence of suitable habitats and corridors (although concrete data are needed on this topic), which are both influenced by local sand- and vegetation dynamics, the species can be used as an indicator for the follow up and evaluation of the contemporary management and the quality of the dune-ecosystem. The maintenance of the species by conservation and restoration of the suitable habitats and by the connection of the fragmented dune entities via suitable dispersal matrices, is of primary importance: extensive grazing in the dune will both create suitable habitats for adults and connect the grassland remnants without eliminating all the hibernation habitats. The maintenance of the species in the young dune slacks is impossible without machined restoration of the habitat. Natural formation of the habitat will soon burn out because of the high amount of dune fragmentation and sand stabilisation, which as a consequence impede sand dynamics.

Population interchange between the different isolated dune entities will probably only occur via migration along coastal Marram dunes. The restoration and conservation of these narrow corridors should be encouraged, especially at the seaside of the larger coastal communities.

REFERENCES

ALDERWEIRELDT, M. & J.-P. MAELFAIT (1988). Life cycle, habitat choice and distribution of *Pardosa amentata* (Clerck, 1757) in Belgium (Araneae, Lycosidae). *Bulletin de la Société scientifique de Bretagne: Comptes rendus du Xème*

Colloque Européen d'Arachnologie, 59 (N° hors série 1): 7-15.

ALDERWEIRELDT, M. & MAELFAIT, J.-P. (1990). Catalogus van de spinnen van België. Deel VII. Lycosidae. *Studiedocumenten van het KBIN*, 61: 92 pp.

ANDREN, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportion of suitable habitat. *Oikos*, 71: 355-366.

ANTEUNIS, A. (1956). Biosociologische studie van de Belgische zeeduinen. Verband tussen de plantengroei en de molluskenfauna. *Verhandelingen van de Koninklijke Academie voor Wetenschappen, Letteren en Schone Kunsten. Klasse der Wetenschappen,* nr. 54: 193 pp.

BAERT, L. & K. DESENDER (1993). De Spinnenfauna van het militair domein te Lombardsijde (Araneae). *Nwsbr. Belg. Arachnol. Ver.*, 8(1): 15-20.

BARKMAN, J.J. & P. STOUTJESDIJK (1987). *Microklimaat, vegetatie en fauna*. Pudoc Wageningen, 223 pp.

BERRY, A.Q., F. GALE, J.L. DANIELS & W. ALLMARK, W. (1996). *Fenn's and Whixall Mosses*. Clwyd County Council, Mold.

BLANDIN, P. (1986). Bioindicateurs et diagnostic des systèmes écologiques. *Bull. Ecol.*, 17: 215-307.

BLANDENIER, G. & P.A. FÜRST (1998) Ballooning spiders caught by a suction trap in an agricultural landscape in Switzerland In: P.A. SELDEN (1998) (ed.). *Proceedings of the 17th European Colloqium of Arachnology*, Edinburgh 1997: 177-185.

BONTE, D. (1997). Het voorkomen van *Hyles euphorbiae, Aricia agestis, Hipparchia semele* en *Issoria lathonia* in het duingebied van de Vlaamse Westkust in 1996 (*Lepidoptera*). *Phegia*, 25 (1):1-5.

BONTE, D. & G. DE KNIJF (1997). Occurrence and habitat preference of grasshoppers (*Saltatoria*) in the Flemish coastal dunes. *Biol. Jb. Dodonea*, 65: 109-110.

BONTE D. & F. HENDRICKX (1997). Aanvullende gegevens omtrent de spinnenfauna van enkele duingebieden aan de Belgische Westkust. *Nwsbr. Belg. Arachnol. Ver.*, 12 (2): 33-43.

BONTE D. & J.-P. MAELFAIT (1998). De levenscyclus van enkele spinnen uit de duinen. *Nwsbr. Belg. Arachnol. Ver.*, 13 (1): 1-14.

BONTE, D., M. HOFFMANN & J.-P. MAELFAIT (1999). Monitoring van het begrazingsbeheer in de Belgische kustduinen aan de hand van spinnen. *Nieuwsbr. Belg. Arachnol. Ver.*, 14 (1): 24-36.

BONTE, D., J.-P. MAELFAIT & M. HOFFMANN (1998). Aeronautisch actieve spinnen in een duingebied te Oostduinkerke. *Nieuwsbr. Belg. Arachnol. Ver.*, 13 (3): 77-85.

BONTE, D., M. HOFFMANN & MAELFAIT, J.-P. (2000a). Seasonal and diurnal migration patterns of the spider fauna of coastal grey dunes. *Ekologia* (Bratislava), 19/4 suppl.: 5-16.

BONTE, D., J.-P. MAELFAIT & M. HOFFMANN (2000b). The impact of intensive cattle grazing on the spider communities *Araneae* in a mesophytic dune grassland. *J. coastal. Conserv.,* 6 (2): 135-144.

CLARKE, K.R. & M. AINSWORTH (1993). A method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser.*, 92: 205-219.

DE BACKER, S.M. (1963). Etudes microclimatiques. II. Dunes littorales – Oostduinkerke août 1951 et juillet-août 1952. *K.M.I. België, Publicaties*, serie A, nr 39, 24 pp.

DE RAEVE, F. (1989a). Sand dune vegetation and management dynamics. In: VAN DER MEULEN, F., JUNGERIUS, P.D. & VISSER, J.H. (red). *Perspectives in coastal dune management*. Academic publishing, Den Haag: 99-110.

DECAE, A.E. (1987). Dispersal: ballooning and other mechanisms. In: NENTWIG W. (ed) (1987). *Ecophysiology of spiders*. Springer Verlag, Berlin, 448 pp.

DECLEER, K. (1998). Temporary inundation as a determining factor for the spider communities of marshland habitats. In: HAUPT, J. (ed). *Comptes Rendus du XIème Colloque d'Arachnologie*, Berlin, 1998: 161-167.

DECLERQ E. & G. DE MOOR (1996). Geomorfologie van de Vlaamse kust. In: PROVOOST, S. & M. HOFFMANN (eds.) (1996). *Ecosysteemvisie voor de Vlaamse Kust*. Universiteit Gent en Instituut voor Natuurbehoud (Brussel), in opdracht van de Vlaamse Gemeenschap (Afdeling Natuur): 48-86.

DELETTRE, Y.R., N. MORVAN, P. TRÉHEN & P. GROOTAERT (1998). Local biodiversity and multi-habitat use in empidoid flies (Insecta: Diptera, Empidoidea). *Biodiversity and Conservation*, 7: 9-25.

DEN HOLLANDER, J. (1971). Life histories of species of the *Pardosa pullata* group, a study of ten populations in the Netherlands (Aranaea, Lycosidae). *Tijdschrift Voor Entomologie*, 114 (8): 255-280.

DENNIS, P., M.B. THOMAS & N.W. SOTHERTON (1994). Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. *J. Appl. Ecol.*, 31: 361-370.

DESENDER K. (1996). Diversity and dynamics of coastal dune carabids. *Ann. Zool. Fennici*, 33: 65-75.

DESENDER, K. & H. TURIN (1989). Loss of habitats and change in the composition of the ground- and tigre beetle fauna in four West European countries since 1950 (Coleoptera, Carabidae, Cicindelidae). *Biol. Conserv.*, 48: 277-294.

DESENDER, K., J.-P. MAELFAIT & L. BAERT (1991). Monitoring Carabid beetles in Belgian Coastal dunes. *Proceedings of the 4th ECE/XII.SIEEC*,Gödöllö: 153-158.

DUFFEY, E. Aerial dispersal in spiders. In: P.A SELDEN (1998) (ed.). *Proceedings of the 17th European Colloqium of Arachnology*, Edinburgh 1997: 187-191.

EDGAR, W.D. (1970). The life cycle, abundance and seasonal movement of the wolf spider Lycosa lugubris in Central Scotland. *J. Animal. Ecol.*, 40: 303-322.

FOELIX, R.F. (1996). *Biology of spiders*. Oxford University Press, Georg Thieme Verlag, 330 pp.

FOUILLET, Ph. (1988). Les Araneides des schorres de la baie du Mont Saint Michel: distibution and rélations avec les facteurs mésologiques. *Bulletin de la Société scientifique de Bretagne: Comptes rendus du Xème Colloque Européen d'Arachnologie*, 59 (N° hors série 1): 65-86.

GREENSTONE, M.H., C.E. MORGAN, A.-L. HULTSCH (1985). Ballooning methodology: equations for estimating masses of sticky-trapped spiders. *J. Archnol.*, 13: 225-230.

HANSKI, I. (1999). *Metapopulation Ecology*. Oxford University Press Inc., New York.

HENDRICKX, F., J.-P. MAELFAIT, W. MUYLAERT & M. HOFFMANN (1998). Spider distribution along the tidal River Scheldt

(Belgium). In: P.A SELDEN (1998) (ed.). *Proceedings of the 17th European Colloqium of Arachnology*, Edinburgh 1997: 265-291.

HILL, J.K., C.D. THOMAS & O.T. LEWIS (1996). Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *J. Animal Ecol.*, 65: 725-735.

HILL, J.K., C.D. THOMAS & O.T. LEWIS (1999). Flight morphology in fragmented populations of a rare butterfly, *Hesperia comma. Biol. Conserv.*, 87: 227-283.

HUBLÉ J. (1975). Arachnofauna van strooisel onder duinstruweel van de Belgische Westkust (soortenlijst). *Biol. Jb. Dodonea*, 43: 146-150.

HUBLÉ J. (1976). Bodemspinnen van duinmoeras en helmduinen in het staatsnatuurreservaat 'De Westhoek' (Soortenlijst). *Biol. Jb. Dodonea*, 44: 226-230.

HUBLÉ J. & J.-P. MAELFAIT (1981). Analysis of the spider fauna from a north and a south-facing slope of a coastal dune (Belgium). *Faun.-Ökol. Mitt.*, 5: 175-189.

JERROLD, H.Z. (1996). *Biostatistical analysis*. Prentice Hall International Editions.

JOY, J. & S. PULLIN (1997). The effect of flooding on the survival and behaviour of overwintering Large Heath Butterfly *Coenonympha tullia* Larvae. *Biol. Conserv.*, 82: 61-66.

KIRCHNER, W. (1973). Ecological aspects of cold resistance in spiders (a comparative study). In: WIESER, W. (1973) (ed). *Effects of Temperature on Ectotherm organisms*. Springer Verlag Berlin: 271-279.

KOEHLER H., E. MUNDERLOH & S. FOFMANN (1995). Soil microarthropods (Acari, Collembola) from beach and dune: characteristics and ecosystem context. *Journal of Coastal Conservation*, 1: 77-86.

KRUSKAL, J.B. & M. WISH (1978). *Multi-dimensional scaling*. Sage Publications, Beverly Hills.

LEGEL, G.J. & W.K.R.E. VAN WINGERDEN (1980). Experiments on the influence of food and crowding on the aeronautic dispersal of *Erigone atrica* (White, 1852) (Araneae, Linyphiidae). In: GRUBER, J. (ed.), 8. *Internationaler Arachnologen Kongress Wien 1980*. Verhandulingen, Eggerman, Vienna: 97-102.

LEJEUNE, R..R., W.H. FELL & D.P. BURBIDGE (1955). The effect of flooding on development and survival of the larch sawfly *Pristiphora erichsonii* (Tenthrenidae). *Ecology*, 36: 63-70.

MAELFAIT J.-P. (1993). Spinnen en natuurontwikkeling in het duinengebied 'Home Theunis' te Oostduinkerke. *Duinen*, 4: 146-154.

MAELFAIT, J.-P. & L. BAERT (1975). Les araignées sont-elles de bons indicateurs écologiques? *Bull. Soc. sci. Bret*, 59 h.s. 1: 155-160.

MAELFAIT J.-P. & L. BAERT (1987). Het gebruik van spinnen bij ecologische indicatie. *Nwsbr. Belg. Arachnol. Ver.*, 6: 24-27.

MAELFAIT, J.-P., M. ALDERWEIRELDT, K. DESENDER, & L. BAERT. (1989). Lycosid spiders of the Belgian Coast. *Bull. Annls. Soc. r. belge Ent.*, 125: 327-332.

MAELFAIT J.-P., BAERT L. & K. DESENDER (1996). Nature conservation management in coastal dunes and spiders. *Proceedings of the 16th European colloquium of arachnology*. Siedlce, Poland: 221-236.

MAELFAIT J.-P., L. BAERT. & K. DESENDER (1998). Effects of groundwater catchment and grassland management on the spider fauna of the dune nature reserve 'De Westhoek' (Belgium). In: P.A. SELDEN (1998) (ed.), *Proc. 17th Europ. Coll. Arachn.*: 221-236.

MAELFAIT, J.-P., L. BAERT, M. ALDERWEIRELDT & M. JANSSENS (1998). A red list for the spiders of Flanders. *Bull. K. Belg. Inst. Natuurwet., Entomologie*, 68: 131-142.

MAELFAIT, J.-P. & F. HENDRICKX (1998). Spiders as bio-indicators of anthropogenic stress in natural and semi-natural habitats in Flanders (Belgium): some recent developments. *Proceedings of the 17th European Colloqium of Arachnology*, Edinburgh 1997: pp. 293-300.

MILLER, G.L. (1984). Ballooning in *Geolycosa turricola* (Treat) and *Geolycosa patellonigra* Wallace: high dispersal frequencies in stable habitats. *Can. J. Zool.*, 62: 2110-2111.

MOUSSON, L., G. NÈVE & M. BAGUETTE (1999). Metapopulation structure and conservation of the cranberry fritillary *Boloria aquilonaris* (Lepidoptera: Nymphalidae) in Belgium. *Biol. Conserv.*, 87: 285-293.

PROVOOST, S. & M. HOFFMANN (eds.) (1996). *Ecosysteemvisie voor de Vlaamse Kust*. Universiteit Gent en Instituut voor Natuurbehoud (Brussel), in opdracht van de Vlaamse Gemeenschap (Afdeling Natuur), 3 parts.

RICHTER C.J. (1970). Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). *Oecologia*, 5: 200-214.

RUSHTON, S.P. 1988. The effect of Scrub Management Regimes on the Spider Fauna of Chalck Grassland, Castor Hanglands National Nature Reserve, Cambridgeshire, UK. *Biol. Conserv.*, 46:169-182.

SCHAMINÉE, J.H.J., A.H.F. STORTELDER & E.J. WEEDA (1995). *De vegetatie van Nederland. Deel 2. Plantengemeenschappen van waters, moerassen en natte heide*. Opulus pres, Upssala-leiden.

SCHAMINÉE, J.H.J., A.H.F. STORTELDER & E.J. WEEDA (1996). *De vegetatie van Nederland. Deel 3. Plantengemeenschappen van graslanden, zomen en droge heiden*. Opulus pres, Upssala-leiden.

SCHAMINÉE, J.H.J., A.H.F. STORTELDER & E.J. WEEDA (1997). *De vegetatie van Nederland. Deel 4. Plantengemeenschappen van pioniers- en kustvegetaties*. Opulus pres, Upssala-leiden.

SEGERS, H. (1989). De levenscyclus van *Pardosa lugubris* (Walckenaer, 1802) in het Zoniënbos (Araneae, Lycosidae). *Nwsbr. Belg. Arachnol. Ver.*, 12: 5-14.

SEGERS, H. & J.-P. MAELFAIT (1990). Field and laboratory observations on the life cycle of *Coelotes terrestris* and *Coelotes inermis* (Araneae, Agelenidae). *Bull. Soc. d'Arachnol.*, 1: 314-324.

SIMBERLOFF, D. (1998). Flagships, umbrellas and keystones: is single-species management passé in the landscape era. *Biol. Conserv.*, 83 (3): 247-257.

SPEIGHT, M.C.D. (1986). Criteria for the selection of insects to be used as bio-indicators in nature conservation research. *Proceedings of the third European Congress of Entomology*, Amsterdam: 485-488.

SUTCLIFFE, O.L., THOMAS, C.D. & D. PEGGIE (1997). Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. *Oecologia*, 109: 229-234.

THOMAS C.F.G. (1996). Modelling aerial dispersal of Linyphiid spiders. *Asp.of Appl. Biol.*, 46: 217-222.

TOFT S. (1976). Life-histories of spiders in a Danish beech wood. *Natura Jutlandica*, 19: 6-39.

VAN DER AART, P.J.M. (1975). D*e verspreiding van wolfspinnen in een duingebied, geanalyseerd met behulp van multivariate technieken*. PhD-thesis, Leiden.

VAN DONGEN, S., L. LENS & G. MOLENBERGHS (1999). Mixture analysis of asymmetry: modelling directional asymmetry, antisymmetry and heterogeneity in fluctuating asymmetry. *Ecol. Lett.*, 2: 387-396.

van WINGERDEN W.K.R.E. & H.F. VUGHTS (1974). Factors influencing aeronautic behaviour of spiders. *Bull. Br. Arachnol. Soc.*, 3 (1): 6-10.

VAN WINGERDEN W.K.R.E. (1980a). Aeronautic dispersal of immatures of two Linyphiid spider species (Araneae, Linyphiidae). *Proc. 8th. Int. Congress of Arachnology*. 1980, Vienna. Verlag H. Egerman, Vienna: 91-96.

VAN WINGERDEN W.K.R.E. (1980b). Experiments on the influence of food and crowding on the aeronautic dispersal of *Erigone arctica* (White, 1852) (Araneae, Linyphiidae). In: GRÜBER J., (ed.). *Proc. 8th. Int.Congress of Arachnology*. 1980, Vienna. Verlag H. Egerman: 92-102.

VERMEERSCH, C. (1986). De teloorgang van de Belgische kust. *Ruimtelijke planning*, 15, II E.2.f. Van Loghum Slaterus, Antwerpen, 37 pp.

VLIJM L. & A. KESSLER-GESCHIERE (1967). The phenology and habitat of *Pardosa monticola, P. nigriceps* and *P. pullata* (Aranaea, Lycosidae). *J. Anim. Ecol.*, 36: 31-56.

VUGHTS H.F. & W.K.R.E. VAN WINGERDEN (1976). Meteorological aspects of aeronautic behaviour of spiders. *Oikos*, 27: 433-444.

WEYMAN G.S. & P.C. JEPSON (1994). The effect of food supply on the colonisation of barlet by aerially dispersing spiders (Araneae). *Oecologia*, 100: 386-390.

WIEBES, J.T. & J. DEN HOLLANDER (1974). Nederlandse wolfspinnen (Lycosidae en Pisauridae). *Wetenschappelijke mededelingen KNNV*, 23 pp.

WONNACOT & WONNACOT (1990). *Introductionary statistics*. John Wiley & Sons, New York.