The impact of grazing on spider communities in a mesophytic calcareous dune grassland

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Abstract. During 1994-1995 and 1997-1998 spiders were sampled with pitfall traps in a botanically rich, mesophytic, calcareous dune grassland in Belgium. As a consequence of intensive cattle grazing, vegetation variation in a large part of the area had diminished. The study area was also patchily grazed by rabbits. Community analysis with TWINSPAN revealed five distinct spider communities. Ecological differentiation was best explained by combination of the habitat variables: distance from grazed or non-grazed vegetation, *Rosa pimpinellifolia* cover and grass cover in both summer and winter. Species diversity was highest in the border zone between the cattle-grazed and non cattle-grazed sites.

Correlation of the most abundant spider species with the vegetation determinants explains the ecological differentiation between the spider communities. Species were classified into seven major groups that reflect the species' habitat preferences. The group showing clear association with non cattle-grazed, tall vegetation consists of common species. Characteristic species for the intensively cattle-grazed sites are common aeronauts and rare species such as *Walckenaeria stylifrons, Mastigusa arietina, Ceratinopsis romana* and *Pardosa monticola*. The latter are shown to be dependent on ungrazed vegetation for juvenile development and overwintering. Intensive grazing results in homogeneous short vegetation, which can only be colonized by 'open ground' species with a well-developed dispersal capacity, or by species which are not dependent on litter-rich situations for juvenile development. An extensive cattle grazing regime results in a patchy mosaic grassland where, in addition to the above mentioned groups of species, other species survive by migrating between the buffered litter rich ungrazed vegetation and the short vegetation. Additionally, some typical and rare species prefer the transition zone between the grazed and the ungrazed vegetation because they are associated with specific habitat structures or inhabiting ant-species.

Keywords: *Araneae*; Dune management; Hibernation habitat; Non-metric multidimensional scaling.

Nomenclature: Roberts (1987, 1995) for *Araneae*; van der Meijden et al. (1990) for vascular plants; Corly et al. (1981) for bryophytes; Schaminée et al. (1996) for vegetation associations.

Introduction

Since the beginning of the 20th century the total area of coastal dunes in Flanders (Belgium) has diminished from ca. 6000 ha to < 3800 ha. These dunes are characterized by an overall increase of competitive plant species such as *Hippophae rhamnoides, Rosa pimpinellifolia* and *Calamagrostis epigejos* which is due to the retreat of local dune farmers following World War II and a decrease of the rabbit population (due to myxomatosis). Reduction of grazing intensity in dry coastal dunes is the determining factor for grass encroachment (Veer 1997); this phenomenon is probably triggered by atmospheric N-deposition and enhanced by positive feedbacks in the nitrogen cycle.

Well-developed mesophytic calcareous dune grasslands (*Polygalo-Koelerion* and *Taraxaco-Galietum*) are rare and threatened in Flanders (Provoost & Hoffmann 1996). Deltschev & Kajak (1974) studied the influence of grazing on the spider fauna and found that intensive grazing completely destroyed the spider assemblage of the former vegetation. De Keer et al. (1989), Maelfait & De Keer (1990) and Gibson et al. (1992) found that heavily grazed pastures were dominated by a group of *Linyphiidae*, characteristic of disturbed land.

Van der Aart (1975), Alderweireldt et al. (1986), Maelfait (1993), Baert & Desender (1996), Bonte (1996) and Maelfait et al. (1997) however, found many typical and interesting species in dune vegetation that was kept short by rabbits (*Oryctolagus cuniculus*). De Keer et al. (1989) suggested that some species, characteristic of short-grazed vegetation, retire to islets of rough vegetation at night. Bonte et al. (2000) found that species of grey dunes are dependent on tall vegetation for juvenile development and hibernation. Therefore, we expect, and will show differences in spider community composition and structure in mesophytic dune grasslands depending on grazing intensity (cattle or rabbits); we will also show the ecological importance of the proximity of rough vegetation.

Material and Methods

Study area

Data were collected in a dune area at Oostduinkerke (Koksijde, West Flanders, Belgium), which was formed in the 11th century as a spit of sandy dunes in the IJzer-estuary. Due to eolic processes, an undulating landscape (*kopjesduin*) was formed (Provoost & Hoffmann 1996). The area has probably been used as pasture by local farmers for centuries (Hoffmann et al. 1998). This land use, in combination with a lime-rich soil, has resulted in floristically rich dune grassland.

The northwestern part of the area is intensively grazed by cattle from May till October (2 - 3 cows/ ha). As a result vegetation height rarely exceeds 10 cm. It is mainly dominated by mosses (e.g. *Tortula ruralis* ssp. *ruraliformis, Hypnum cupressiforme* var. *lacunosum)*, low scattered grasses (e.g. *Poa pratensis, Agrostis capillaris),* sedges (e.g. *Carex arenaria)* and mesophytic herbs (e.g. *Galium verum, Asperula cynanchica, Helianthemum nummularium, Potentilla neumanniana* and *Rumex acetosella).* No nitrogen fertilization takes place. The remaining part of the area has, in part, been grazed by cattle or horses in the past but recently has been grazed only by rabbits, small rodents and invertebrates. Depending on the intensity of rabbit grazing, the grass layer height varies between 5 and 60 cm. The rabbit-grazed, short vegetation patches (a few acres) are characterized by similar vegetation as the intensively cattle-grazed pasture. Vegetation not grazed by cattle or rabbits can be divided into two types: (1) grassland dominated by *Arrhenatherum elatius* and *Calamagrostis epigejos* and (2) dwarf scrub dominated by *Rosa pimpinellifolia*, both have a well-developed litter layer. Typical grassland species including *Rhinanthus minor, Achillea millefolium* and nitrophilic species such as *Rubus caesius* and *Urtica dioica* regularly appear in the grassland vegetation. Typical in the dwarf scrub vegetation are a well-developed moss layer and a less dense grass layer. Scrub vegetation with *Hippophae rhamnoides* and *Salix repens* is rare and scattered in the study area.

Methodology

Spiders were trapped by using pitfalls (Table 1). The different grazing regimes with associated vegetation types are called treatments. Two rows of three pitfalls (numbered 1 – 3) were placed at each station as follows:

Treatment A: Cattle-grazed grassland
   Station A1: One row 10 – 15 m from the non cattle-grazed area. The vegetation was dominated by mosses: *Hypnum cupressiforme* var. *lacunosum* (60 - 70 % cover), *Poa pratensis* (10 - 20% cover) and *Potentilla naumanniana* (5 - 20% cover). Due to cattle trampling 5 - 10 % bare sand was present around the traps.

   Station A2: One row ca. 150 m from the non cattle-grazed area. Vegetation as in A1.
Treatment B: border of the cattle-grazed area, patchily grazed by rabbits.
   Station B: Heterogeneous grassland dominated (over 80 %) by dense *Avenula pubescens* (B2) and *Calamagrostis epigejos* (B3) vegetation. One pitfall (B1) was placed in a small patch, short-grazed by rabbits and characterized by similar vegetation as stations A1 & A2.
Treatment C: Tall, dense dune grassland, not grazed by cattle but sporadically by rabbits
   Station C1: One row in a dense and 20 - 35 cm tall *Rosa pimpinellifolia* vegetation (100 % cover; litter layer maximally 10 cm.
   Station C2: One row in biennially mown grassland aimed at orchid-conservation (summer height max. 45 cm). Low *Salix repens* (30 - 40 % cover), *Arrhenatherum elatius* (10 - 20 % cover) and *Festuca rubra* (10 - 20 % cover) dominated the vegetation. In contrast with C and B2 and B3, almost no grass litter was present in this site, due to removal of the mown vegetation. The moss *Brachythecium albicans* had a cover of 5 - 20 % in the undergrowth.

We only used three pitfall traps per treatment since this is sufficient for sampling the prevalent spider species (Stein 1965; Kabacik-Wasylik 1970). This is also the absolute minimum for the application of non-parametric statistics (Siegel & Castellan 1988). The pitfall arrays A1, A2 and B were emptied fortnightly from March 1997 until March 1998. C1 and C2 were censused from April 1994 until April 1995, within the framework of an earlier invertebrate survey. A 4% formalin-detergent solution was used as a fixative in the pitfalls.

In summer 1997 and winter 1998, phytosociological relevés using the Londo (1975) scale were made around all pitfall traps. The vegetation height was measured 10 times at random around each trap, mean height and standard deviation were calculated later. The distance to the nearest dense ungrazed (positive) or short-grazed (negative) vegetation was measured, since this could be an important community-determining factor. Only those plant species which determined vegetation structure (i.e. *Rosa pimpinellifolia, Calamagrostis epigejos*), were included in the environmental data set. Two other vegetation structure parameters were included in the analysis: the total cover of the non-overgrown moss layer (mainly *H. cupressiforme* var. *lacunosum*) and the total cover of mesophytic vascular plants (cover of the herb layer) in advance of integration into the data set (Table 2). These vegetation and distance parameters are labelled

Table 1. Description of the different treatments A1 - C2. Every treatment is sampled fortnightly with three pitfalls.

	Grazing type	Observation period	Remarks
A1	Cattle-rabbits	03/97-03/98	10 - 15 m from non cattle-grazed area
A2	Cattle-rabbits	03/97-03/98	150 m from non cattle-grazed area
B	Rabbits/none	03/97-03/98	patchy dune grassland vegetation
C1	None	04/94-04/95	dwarf scrub of *Rosa pimpinellifolia*
C2	None	04/94-04/95	irregularly mown tall grassland

habitat variables. Topography of the sampling stations was derived from digital topographic terrain maps, made at the Institute of Nature Conservation (Brussels).

Community composition and environmental variables

We did not use Canonical ordination techniques (Hill 1979a) to interpret differences in community structure as a result of differences in species composition, because the assumption of a linear relationship among and between the biotic and environmental variables (Clarcke & Ainsworth 1993) is not appropriate: many animal species show a logistic distribution in relation to abiotic parameters. A more natural configuration is obtained when rank-order relationships are used to compare samples. This was done in *Non-metric multidimensional scaling* (MDS) with the Bray-Curtis similarity measure as a rank-order relation coefficient (Clarcke & Ainsworth 1993) using the statistical package PRIMER (Carr et al. 1993; Clarcke 1993) with consecutive harmonic rank and Spearman rank correlation factors between the MDS-ordinations of both the biotic and the various combinations of environmental data.

In order to determine characteristic (indicator) species for the communities recognized, an additional TWINSPAN analysis (Hill 1979b) was carried out.

Statistical analysis was performed with the STATISTICA 5.1 software package. Analysis of differences between the ungrazed and grazed treatments and between the grazed treatments close to, and far from, the rough vegetation were performed with a Mann-Whitney U-test. Spearman correlation calculations were used for the detection of relationships between species numbers and the relevant environmental data and for the relationship between expected species richness per 100 caught individuals and species numbers. A Kruskal-Wallis ANOVA was applied for the comparison of mean species richness between all treatments.

Results

Community composition and its determining environmental variables

A total of 92 species were captured over the sampling period, 33 species with less than three individuals (Table 3). Only the remaining 59 species were included in the community composition analysis. In order to compare the species assemblages in the five different treatments, the data were transformed to relative abundance, by equal weighting of all species caught in the traps.

The outcome of the MDS-ordination (stress factor 0.091) is shown in Fig. 1. All five treatments can be clearly distinguished, arranged along a gradient from the short-grazed dune grassland to the rough grassland. Linkage of the environmental data to the species data reveals the determining habitat variables (Table 4). The best explaining subset (Harmonic rank correlation) is the combination of distance from the cattle-grazed or non cattle-grazed vegetation, *Rosa pimpinellifolia* cover and cover of the grass and herb layer in both summer and winter.

TWINSPAN analysis reveals three indicator species: *Mastigusa arietina* in the transition zone, *Typhochrestus digitatus* in the low, grazed vegetation and *Argenna subnigra* in the non cattle-grazed treatments with tall vegetation.

Species which show a significant correlation (Spearman rank correlation, $p < 0.05$) with at least one of the community-determining variables are shown in Table 5. Typical species of tall and dense vegetation (significant positive Spearman rank correlation with summer and winter cover and *R. pimpinellifolia* cover respectively) are *Bathyphantes gracilis*, *Pardosa nigriceps* and *Trochosa terricola*. The numbers of individuals of several species increase with increasing *Rosa pimpinellifolia* or grass cover (both during the summer and the winter), e.g.

Table 2. Measured habitat variables surrounding the different pitfall traps (see Table 1).

Trap	DI	RP	CE	HL	BS	MO	WC	SC	HE	TO
A1-1	8	0	1	20	10	70	20	20	8.54 (2.54)	7
A1-2	7	2	1	20	5	75	20	20	8.27 (2.41)	7
A1-3	3	3	5	25	10	60	30	40	10.54 (3.83)	7
A2-1	175	0	0	25	5	70	25	60	7.90 (1.81)	7.5
A2-2	175	0	0	20	5	75	20	55	8.27 (1.61)	7
A2-3	175	0	0	25	5	70	25	70	7.90 (4.54)	7
B1	1	5	0	25	5	80	15	40	15.45 (4.00)	7
B2	0	5	0	35	0	65	35	85	24.45 (4.82)	7
B3	-2	45	45	90	0	30	70	95	44.81 (7.11)	7
C1-1	-35	55	0	45	0	55	45	75	15.09 (3.96)	7
C1-2	-35	55	0	45	0	55	45	75	15.18 (3.62)	7
C1-3	-40	55	0	45	0	55	45	75	15.90 (4.36)	7
C2-1	3	0	0	75	0	25	75	85	23.72 (4.54)	6.5
C2-2	3	0	0	75	0	25	75	85	24.81 (6.79)	6.5
C2-3	3	0	0	75	0	25	75	85	25.90 (2.98)	6.5

DI = distance from ungrazed and tall vegetation (where prefixed by a negative sign: distance from short vegetation)
RP = cover (%) of *Rosa pimpinellifolia*
CE = cover (%) of *Calamagrostis epigejos*
HL = cover (%) of the mesophytic grass and herb layer
BS = cover (%) of bare sand
MO = cover (%) of non-overgrown mosses
WC = total winter cover (%) of higher plants
SC = total summer cover (%) of higher plants
HE = vegetation height (mean ± standard deviation) (cm)
TO = topography (meters ATW)

Lepthyphantes tenuis, Ozyptila simplex and *Tapinocyba praecox*. Species that are negatively correlated with this variable include *Erigone atra, Pardosa monticola* and *Pelecopsis parallella. Ceratinopis stativa* seems to avoid *Rosa pimpinellifolia* vegetation ($p < 0.05$). The numbers of individuals of, *i.a.*, *Argenna subnigra* and *Pachygnatha degeeri* show only a significant positive rank correlation with the presence of *Rosa pimpinellifolia*.
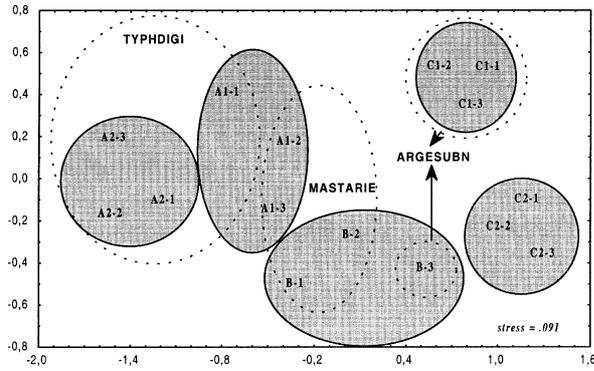
The TWINSPAN classification of the 59 more abundant species (Table 5) clearly separates one group containing species positively correlated with tall grass and *Rosa pimpinellifolia* cover and negatively with distance-to-rough-vegetation measurement (group 1). This first group is subdivided into a group with species positively associated with a high grass-layer and a group also positively correlated with *R. pimpinellifolia* cover. The other two subgroups include species with positive associations with vegetation structure.

The second major division includes species typical of non-shaded and short vegetation that are positively correlated with increasing distance from the tall, rough vegetation and negatively with the cover of summer and

Table 3. Species list of spiders caught in the watertraps (WT) and in the five pitfall stations (A1, A2, B, C1 and C2; see Table 1). * = only immature spiders captured; ° = Immature and adult spiders captured.

Species	WT	A1	A2	B	C1	C2
Agelena labyrinthica	0	0	0	1	0	0
Agroeca cuprea	0	6	0	9	6	1
Agroeca proxima	0	0	1	17	5	5
Agyneta subtilis	0	0	1	0	0	0
Alopecosa barbipes	0	20	9	16	3	8
Alopecosa cuneata	0	11	2	40	15	26
Alopecosa pulverulenta	0	10	5	24	6	16
Arctosa perita	0	2	0	0	0	0
Argenna subnigra	4	0	5	12	17	0
Bathyphantes gracilis	°125	2	3	5	12	7
Bathyphantes parvulus	*2	0	1	0	6	0
Centromerita bicolor	0	2	0	2	0	2
Centromerita concinna	0	67	33	60	0	77
Centromerus prudens	1	5	0	15	5	3
Centromerus sylvaticus	0	3	0	15	34	25
Ceratinopsis romana	4	2	0	1	0	0
Ceratinopis stativa	0	0	0	8	1	0
Cheiracanthium virescens	0	2	0	0	0	0
Clubiona diversa	0	0	0	1	0	0
Clubiona pseudoneglecta	0	0	0	1	2	2
Clubiona frisia	0	1	0	0	0	0
Clubiona subtilis	*4	0	0	1	0	0
Clubiona trivialis	0	0	0	0	2	0
Cnephalocotes obscurus	0	0	0	1	0	0
Dicymbium nigrum	0	1	1	3	0	5
Drassodes cupreus	0	1	0	1	0	3
Drassodes lapidosus	0	1	1	8	0	0
Enoplognatha ovata	0	0	0	1	0	0
Enoplognatha thoracica	0	2	0	4	6	1
Episinus angulatus	0	0	0	1	0	1
Erigone atra	75	165	88	21	7	0
Erigone dentipalpis	16	56	23	19	1	0
Ero cambridgei	0	0	0	0	0	1
Ero furcata	0	0	0	4	1	0
Euophrys frontalis	0	0	0	0	0	1
Floronia bucculenta	0	0	0	1	0	1
Gonatium rubens	0	0	0	5	0	0
Haplodrassus dalmatensis	*1	3	10	3	0	0
Heliophanus cupreus	0	0	0	1	0	0
Heliophanus flavipes	0	0	0	4	0	2
Hypsosinga albovittata	0	1	1	0	0	0
Lepthyphantes pallidus	0	0	0	0	0	1
Lepthyphantes tenuis	*137	6	13	15	38	48
Linyphia triangularis	0	0	0	1	0	0
Lophomma punctata	0	1	0	3	0	0
Maso gallicus	1	0	0	0	0	0
Maso sundevalli	2	0	0	0	0	0
Mastigusa ariëtina	0	2	0	3	0	0
Meioneta rurestris	11	12	21	0	0	0
Meioneta saxatilis	0	0	0	0	4	6
Monocephalus fuscipes	0	1	0	0	0	0
Nereine clathrata	0	0	0	0	1	0

Species	WT	A1	A2	B	C1	C2
Oedothorax apicatus	0	0	1	0	0	0
Oedothorax fuscus	1	0	1	0	0	0
Oedothorax retusus	0	0	1	1	0	0
Ozyptila atomaria	0	2	1	2	5	3
Ozyptila simplex	*14	11	1	21	9	30
Pachygnatha degeeri	0	29	2	21	21	49
Pardosa amentata	0	0	0	0	1	0
Pardosa monticola	0	158	93	56	3	1
Pardosa nigriceps	*3	4	0	18	110	15
Pardosa pullata	0	7	2	5	2	6
Pelecopsis nemoralis	0	3	4	4	0	0
Pelecopsis parallela	0	98	73	3	1	0
Phlegra fasciata	0	3	0	0	0	4
Pirata latitans	*°1	1	0	0	0	0
Pisaura mirabilis	0	3	0	1	2	2
Pocadicnemis juncea	0	1	0	9	29	12
Robertus lividus	0	0	1	6	0	0
Stemonyphantes lineatus	0	13	0	8	15	25
Tapinocyba praecox	0	3	1	16	6	9
Tegenaria agrestis	0	0	1	0	0	0
Thanatus striatus	0	0	0	1	0	0
Theridion bimaculatum	*8	0	0	1	0	2
Tiso vagans	2	1	1	1	0	7
Trachyzelotes pedestris	0	0	0	3	1	1
Trichopterna cito	0	11	30	19	0	0
Trochosa terricola	0	18	1	64	233	186
Troxochrus scabriculus	0	0	1	0	0	0
Typhochrestus digitatus	0	24	33	5	0	0
Walckenaeria acuminata	0	1	0	1	0	0
Walckenaeria antica	0	0	0	1	2	4
Walckenaeria atrotibialis	0	0	0	11	10	3
Walckenaeria monoceros	0	0	2	1	0	0
Walckenaeria nudipalpis	0	0	0	1	0	0
Walckenaeria stylifrons	0	1	1	1	0	0
Walckenaeria unicornis	0	0	1	0	0	0
Xysticus cristatus	1	18	3	21	9	1
Xysticus erraticus	1	7	0	11	5	7
Xysticus kochi	1	41	24	33	0	0
Zelotes electus	0	9	18	21	6	5
Zelotes longipes	0	0	0	1	0	0
Zora spinimana	0	0	0	2	0	1
Araneidae spec.	*1					
Arctosa leopardus	*1					
Clubiona spec.	*8					
Erigoninae spec.	*8					
Heliophanus spec.	*1					
Meta spec.	*1					
Philodromus spec.	*21					
Theridion spec.	*1					
Xysticus spec.	*14					

Fig. 1. Non-metric multi-dimensional scaling of the pitfall traps and superposition of the indicator species, determined by TWINSPAN. Pitfall traps are indicated by their code (see Table 1). Indicator species: TYPHDIGI: *Typhochrestus digitatus*; MASTARIE: *Mastigusa arietina*; ARGESUBN: *Argenna subnigra*.

winter vegetation. Group 01 contains species without clear correlation with the environmental parameters involved, while the remaining groups comprise of species typical of grazed, short vegetation. Only group 001 is characterized by species with a negative correlation with grass-layer coverage.

Impact of cattle grazing on the spider assemblages

Since total numbers of trapped spider individuals per pitfall are positively correlated with the number of different species per pitfall (Spearman correlation, $R = 0.566$; $p = 0.004$), an estimate of species richness was made by transforming the observed number of species per trap into an 'expected' number of species per 100 trapped individuals (Fig. 2). Stations B and C2 are characterized by the highest species richness, while species richness in the three others is approximately equal. Kruskal-Wallis ANOVA of the data of the five stations revealed no overall difference in expected species numbers per treatment ($p > 0.05$), although standard deviations do not overlap between B or A2 and B and C1.

Species which take significant advantage of intensive grazing (U test, $p < 0.05$) include *Erigone atra, Pardosa monticola* and *Pelecopsis parallella* (Table 5). In contrast, *Bathyphantes gracilis, Lepthyphantes tenuis,* and *Pardosa nigriceps* benefit from a rough and non cattle-grazed grass layer. The 'distance from rough vegetation' is an important factor, which determines the presence of certain species of the short-grazed grasslands: e.g. *Centromerus sylvaticus, Trochosa terricola* and *Xysticus cristatus*, occur in significantly (U-test, $p < 0.05$) higher numbers in the proximity of taller (denser) vegetation. Only *Trichopterna cito* has a higher (U-test, $p < 0.05$) population density with increasing distance from the ungrazed areas (Table 5).

The temporal activity patterns (number of individuals caught per treatment per month) for the typical open ground species *Pardosa monticola* in treatments B, A1 and A2 are presented in Fig. 3. Although total catch numbers are different, it is possible to distinguish two activity peaks in the treatments A1 and A2 and only one in B. The first peak can be assumed to be due to active searching for copulation partners. Female activity causes the second peak, as they search for optimal micro-climatological breeding conditions (Bonte 1996). Since rabbit grazing is insufficient (due to a small population size) to keep the vegetation short in late spring, *P. monticola* disappeared in the B station explaining the lack of a second activity peak. On the contrary, cattle-grazing ensures short vegetation during the whole season resulting in the continuous presence of this Lycosid-spider.

The time period in which the first activity peak appears in the three treatments varies. The second peak in July appears in both the two cattle-grazed stations, suggesting a regular distribution of this species all over the habitat. Consequently, we may interpret the three spatially and temporally succeeding activity peaks as seasonal migration of adults of *P. monticola* from the hibernation habitat (rough, non-cattle-grazed edge) to the reproduction habitat (short-grazed dune grasslands).

Table 4. Best variable combinations and the percentage explaining value of the MDS ordination. Bold: the best explaining subset of habitat variables. For key to the habitat variables: see legend Table 2.

Harmonic rank correlation (weighted Spearman)				
k	**Best variable combinations (ρ_w)**			
1	WC (0.553)	DI (0.489)	SC (0.375)	HE (0.294)	TO (0.247)
2	DI, WC (0.724)	DI, SC (0.614)	DI, TO (0.555)	RP, WC (0.527)	
3	DI, RP, WC (0.737)	DI, WC, SC (0.727) DI, SC, TO (0.651) DI, WC, TO (0.633).....			
4	**DI, RP, SC, WC (0.774)**	DI, RP, WC, TO (0.675)	DI, RP, SC, TO (0.672)...		
5	DI, RP, SC, WC, TO (0.738) DI, RP, WC, SC, HE (0.715)....				
6	DI, RP, SC, WC, HE, TO (0.711)	DI, RP, CE, SC, WC, HE (0.593)			

Table 5. Species classification into ecological groups using TWINSPAN and associations of the abundant spider species with the treatment characteristics:

Species	GR U-G	DE C-F	DI	RP	WC	SC	
				Correlation			
Theridion bimaculatum					++	++	
Walckenaeria antica					++	++	
Meioneta saxatilis	U				+	+	111
Clubiona pseudoneglecta					++	++	
Walckenaeria atrotibialis				++	++	++	
Pardosa nigriceps	U		-	++	++	++	
Bathyphantes parvulus	U			++			
Ero furcata				+	+	++	
Trochosa terricola	U	C	—	+	++	++	
Trachyzelotes pedestris						++	
Pocadicnemis juncea	U		-	++	++	++	
Centromerus sylvaticus	U	C	-	+	++	++	
Agroeca proxima					++	++	110
Zora spinimana				+			
Lepthyphantes tenuis	U				++	++	
Pisaura mirabilis					+		
Ozyptila simplex					++	++	
Heliophanus flavipes					++	++	
Tapinocyba praecox					++	++	
Stemonyphantes lineatus	U	C		+			101
Ozyptila atomaria							
Bathyphantes gracilis	U		+		++	+	
Pachygnatha degeeri				+			
Centromerus prudens				+			
Alopecosa cuneata						+	
Tiso vagans							
Phlegra fasciata							
Drassodes cupreus							
Dicymbium nigrum							100
Xysticus erraticus		C					
Alopecosa pulverulenta					+	+	
Gonatium rubens							
Enoplognatha thoracica				++			
Argenna subnigra				++			
Agroeca cuprea		C		++			
Pardosa pullata							
Centromerita bicolor							
Zelotes electus							01
Robertus lividus							
Alopecosa barbipes							
Xysticus cristatus		C	-				
Drassodes lapidosus							
Ceratinopsis stativa			-				000
Pelecopsis nemoralis	G						
Centromerita concinna							
Erigone atra	G		+	-			
Walckenaeria stylifrons							
Meioneta rurestris	G		++				
Walckenaeria monoceros							
Typhocrestus digitatus	G		++	-			
Trichopterna cito	G	F	++				
Pelecopsis parallella	G		++	-			001
Pardosa monticola	G		-	-			
Xysticus kochi	G						
Haplodrassus dalmatensis	G						
Erigone dentipalpis	G		+				
Mastigusa arietina							
Lophomma punctata							
Ceratinopsis romana							

Dendrogram groupings: 111, 110 → 11; 101, 100 → 10; 11, 10 → 1; 01, 000, 001 → 00; 01 and 00 → 0.

Results of the Mann-Whitney U-test (significance level: $p < 0.05$), testing for specific habitat preferences.

GR: Grazing regime: preference for cattle-grazed treatments: G; preference for non-cattle-grazed treatments: U

DE: Distance from rough vegetation: preference for treatment close by the rough vegetation: C; preference for the treatment far from the rough vegetation: F.

Spearman correlations to the distance to the rough vegetation (DI), cover of *Rosa pimpinellifolia* (RP), total cover of the higher plants during the summer (SC) and the winter (WC).

Negative correlation: -: $p < 0.05$; —: $p < 0.01$ and positive correlation:+: $p < 0.05$; ++: $p < 0.01$

Discussion

There is a general consensus that spiders are good ecological indicators (Maelfait & Baert 1988; Rushton 1988; Speight 1986; Maelfait et al. 1989). A commonly used method for sampling is pitfall trapping. Although this methodology has widely known defects, it is a very practical way to sample ground active invertebrates. Since absolute pitfall catches reflect mainly animal activity (for instance ground active species are more frequently caught than typical species of the herb layer) rather than the animal density (Uetz & Unzicker 1976), a transformation of the data to relative activities (number of species caught per trap divided by the total caught numbers during the sampling campaign) is necessary to make comparisons between sampling stations, using species with different activity characteristics. Merrett (1983) showed that even in complex vegetation structures, the spider community composition obtained by pitfall catches (transformed to relative abundance) was broadly similar to those obtained by absolute methods such as D-vacuum suction sampling. By the application of the latter sampling technique, absolute species numbers are obtained which reflect the actual spider densities in the field.

Although we sampled during two different periods, earlier research revealed that the (dominant) spider community composition of stable environments (heathlands, grassland systems, shrubs, woodlands; Baert & Desender 1996; Toft pers. comm.) remains similar from year to year. On the other hand, the composition of spider communities in highly dynamic systems (*Ammophila* dunes, inundated dune slacks) can undergo strong temporal fluctuations, mainly due to changes in the density of typical and dominant opportunistic species (typical of highly disturbed environments). Their colonization is dependent on favourable weather circumstances since they disperse mainly via 'ballooning' (Richter 1970; Bonte et al. 1998). This 'ballooning' or aeronautic behaviour is a passive aerial dispersal of spiders; attached on a long spinneret thread they are transported with moderate air currents on warm, dry days.

The TWINSPAN- and MDS-analyses clearly reveal spider assemblages that differ between the grazed and ungrazed sites, along a more or less continuous gradient from heavily grazed vegetation without nearby rough vegetation, through the transition zone between the areas to the ungrazed and rough vegetation. The coupling of the species data to the environmental data set with the PRIMER software shows the community determining variables. Cattle grazing during the growing season (i.e. summer) directly influences the grass and herb layer, and the presence of the dwarf shrub *Rosa pimpinellifolia*. The tall grass layer and the dwarf shrub layer are both
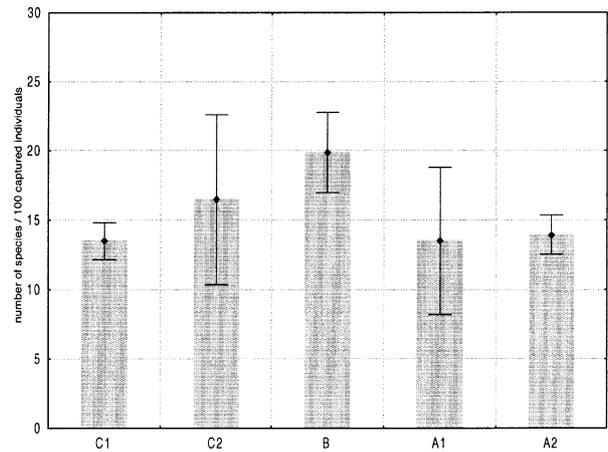
Fig. 2. Mean species richness and standard deviations in the five sample stations (see Table 1), after standardisation to number of species per 100 individuals.

absent from the cattle-grazed area. Rabbit grazing mainly affects the grass layer in the cattle excluded zones. It results in patchy vegetation with alternation of tall grasses, *Rosa pimpinellifolia* and low dune grassland similar to the cattle-grazed situation. The last determining factor is 'distance from rough vegetation', which is responsible for differences in spider communities and total catch numbers. These results are in agreement with the results of other authors who have investigated spider communities in relation to vegetation structure (Rushton 1988; Maelfait et al. 1990; Gibson et al. 1992; Mc Ferran et al. 1994; Maelfait et al. 1997).
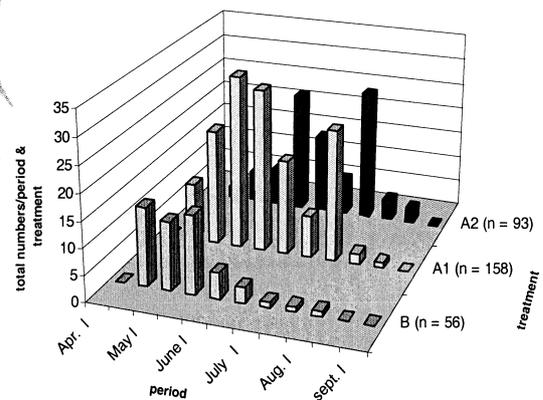
Fig. 3. Activity patterns of the Lycosid spider *Pardosa monticola* in the gradient stations B, A1 and A2 (*n* = number of individuals per treatment).

The intensively cattle- and patchily rabbit-grazed mesophytic dune grasslands are characterized by numerous spider species that are rare on a national scale and are listed on the Flemish Red List of spiders (Maelfait et al. 1998): *Ceratinopis stativa, Haplodrassus dalmatensis, Pardosa monticola, Pelecopsis nemoralis, Trichopterna cito* and *Typhochrestus digitatus*. These species all benefit from short vegetation since they are non-web-building species with a wandering and hunting strategy. *Haplodrassus dalmatensis* is known especially from sandy places and probably benefits from the increase in number and area of trampled vegetation patches in the cattle-grazed dune grassland. Although not caught in large numbers, *Arctosa perita* also benefits from the presence of these patches since it is known to have a burrowing life-style. Additional typical species are those with well-developed aeronautic behaviour: *Erigone atra, E. dentipalpis* and *Meioneta rurestris*. The latter are very common in disturbed habitats (maize and ryegrass fields: Alderweireldt 1989; pastures: Maelfait & De Keer 1990) and highly managed (mowed), temporary ley sites (Rushton et al. 1987). They also occur in large numbers in yearly mown dune slacks (Maelfait 1993; Bonte 1996; Maelfait et al. 1997).

On the other hand, species typical of the non-cattle-grazed, tall, rough vegetation are widespread and occur in a variety of litter-rich and/or shaded inland habitats (different kinds of woodlands), (De Bakker et al. 1998). Species belonging to this group are characterized by a life-style associated with the higher grass layer for web placement (*Theridion bimaculatum, Bathyphantes parvulus*) or epiphytic hunting (*Clubiona pseudoneglecta, Pardosa nigriceps, Ero furcata, Agroeca proxima, Zora spinimana, Heliophanus flavipes*). *Bathyphantes gracilis* and *Lepthyphantes tenuis* are two other aeronautic species, which were caught in significantly larger numbers in the pitfalls in the ungrazed sites than in the grazed treatments. Alderweireldt (1994) investigated the web placement of the latter and found a significantly greater web surface in comparison with those of *Erigone* species. Larger webs need a more complex vegetation structure for attachment. Since intensive grazing shortens the whole grass sward, attachment points disappear. Both species (*B. gracilis* and *L. tenuis*) were, however, caught in large numbers in a watertrap which was placed in analogous short-grazed, moss rich dune grassland, suggesting the dominance of aerial activity in unsuitable habitats (no vegetation for web placement and consequently no prey-capture possibilities) (Bonte et al. 1998).

Due to the presence of different spider assemblages in the short-grazed and rough vegetation, respectively, a higher alpha diversity is obtained in the transition zone. Distance from the dense and ungrazed vegetation seems to be especially important for typical species of the border zone between the grazed and ungrazed zones (for example the rare myrmecophytic species *Mastigusa arietina*) or for species from rougher vegetation, which regularly appear in short-grazed vegetation for prey capture or mating (*Agroeca cuprea, Centromerus sylvaticus, C. prudens, Trochosa terricola, Xysticus cristatus* and *X. erraticus*). *M. arietina* lives in the Flemish coastal dunes in nests of *Lasius niger* and *L. flavus* ants, which are mainly found in the border between cattle-grazed and ungrazed (non-trampled) vegetation (Bonte unpubl.). This species is also found in similar border vegetation types in two other dune areas along the Flemish coast (Bonte unpubl.).

Although many typical 'open ground' species of the short-grazed grassland do not show habitat preference for one of the two cattle-grazed treatments (far from or close to the non cattle-grazed zone), the importance of dense vegetation can be illustrated by reconstructing their relative activity pattern. The Lycosid spider *Pardosa monticola* shows a clear spring migration from the rougher, rabbit-grazed patches to the short and cattle-grazed pasture. Maelfait & De Keer (1990) observed the same seasonal migration between a rough, litter-rich border zone and an intensively grazed pasture for the related species *P. amentata* and *P. pullata* and the Linyphiid species *Centromerita bicolor*.

Pardosa monticola is a typical species of the rabbit-grazed grasslands in coastal and inland dunes (Alderweireldt et al. 1985) and has a typical *Pardosa* life cycle at our latitude, which is mixed annual / biannual (Bonte & Maelfait 1998). It is present only during the summer season on the short-grazed vegetation, where it reproduces. During the colder winter season, it retreats into the rougher (and richer in litter) islets or border zones (Bonte 1996). Those zones are characterized by higher humidity and smaller microclimatic fluctuations. Since the presence of a suitable hibernation habitat is of primary importance for its survival, seasonal migration from the short-grazed to the rougher patches in autumn and in the opposite direction in spring will also be essential. This paper proves the seasonal responses of only one Lycosid species. Many species of the same guild probably show these migrations patterns and will, consequently, be directly dependent for their survival on ungrazed islets of rough vegetation.

Nature management in the Flemish coastal dunes is mainly based on botanical values of the specific sites. Since mown dune slacks and mesophytic grasslands contain the most threatened plant species (e.g. orchids such as several *Dactylorhiza* species, *Herminium monorchis* and other species such as *Parnassia palustris* and *Equisetum variegatum*) large areas are rigorously mown each year. As a consequence, many spider species of the

rougher islets are threatened with extinction from the managed sites (Maelfait et al. 1997). The value of rough and litter-rich zones as hibernation or juvenile development habitat for species typical of the short-grazed sites or as an intrinsic habitat for litter-preferring species should be stressed. Gibson et al. (1992) stated that large web spinners are most sensitive to grazing, preferring ungrazed controls because of their dependence on rigid structures. Although the ungrazed plots contained maximum spider diversity, Ratcliffe (1977) and Duffey (1978) also found that numerous species characteristic of heathland, calcareous grassland or dunes are restricted by the need for short open turf or bare soil. Rushton et al. (1989) evaluated the dramatic effect of pasture improvement on ground beetle and spider communities of upland grasslands. Those assemblages were comparable with those of intensively managed pastures at lower altitudes. Morris (1968) studied the effect of grazing on the fauna of chalk grasslands in Great Britain, finding a clear lowering of total densities of *Gastropoda, Isopoda, Arachnida, Myriapoda, Hemiptera, Thysanaoptera* and *Coleoptera*. The author also proved the dependence of some species (e.g. *Apion dichroum,* Coleoptera, Apionidae) on both types of grassland: hibernation in the rough sites as larvae and the use of the grazed sites in the adult phase.

According to van Den Bos & Bakker (1990), cattle grazing in mixed *Arrhenatherion-Lolium* pastures at low stock density produces a stable vegetation pattern incorporating both short-grasslands (ca. 75% cover) and stands with hardly any short turf within four years. The patterns were significantly correlated with the patterns of terrain use, derived from the number of dung patches. Since nature management aims at optimization of biodiversity, dune grassland management by maintaining cattle grazing at low stocking density would surely achieve a larger faunal and floral diversity in these grassland systems than can be expected from regularly and entirely mown systems or from intensively grazed grasslands.

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