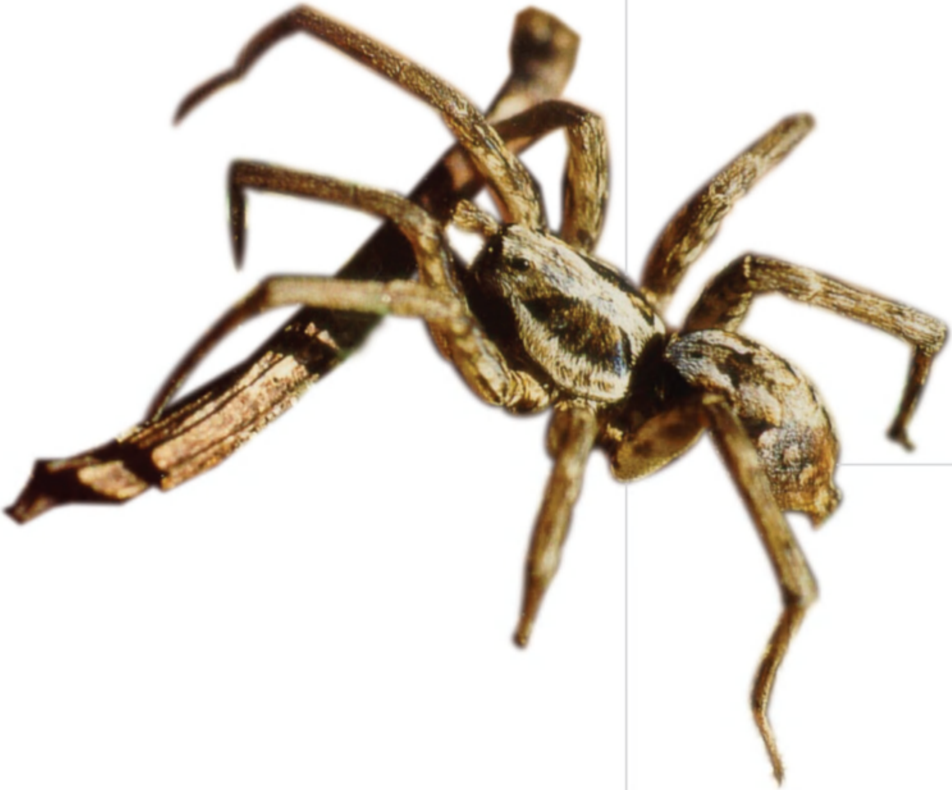
Distribution of spiders in coastal grey dunes

SPATIAL PATTERNS AND EVOLUTIONARY-ECOLOGICAL IMPORTANCE OF DISPERSAL

Dries Bonte



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Distribution of spiders in coastal grey dunes:
spatial patterns and evolutionary-ecological importance of dispersal

Verspreiding van spinnen in grijze kustduinen:
ruimtelijke patronen en evolutionair-ecologisch belang van dispersie

door

Dries Bonte

Thesis submitted in fulfilment of the requirements for the degree of Doctor [Ph.D.] in Sciences

Proefschrift voorgedragen tot het bekomen van de graad van Doctor in de Wetenschappen

Promotor: Prof. Dr. E. Kuijken

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1.1 THESIS OUTLINE AND INTRODUCTION

FOTO: DRIES BONTE

Objective and outline of the thesis

This Ph.D. study contributes to the '*Nature management monitoring programme of the Belgian coastal dunes*' [1996-2002]. This programme is based on a multidisciplinary, integrated approach. The three main research entities participating in this programme are the Laboratory of Soil Science and Terrestrial Ecology Unit of Ghent University and the Institute of Nature Conservation [Section Landscape Ecology and Nature Management]. The motherproject was funded by the Ministry of the Flemish Community, AMINAL, department Nature and initially [1996-1999] cofinanced by the LIFE-project 'Integrated Coastal Conservation Initiative [ICCI]'. The primary aim of the monitoring programme is to evaluate the results of the applied nature management measures, especially grazing by domestic livestock, in the coastal dunes, but additional research projects were started up in the Terrestrial Ecology Unit of Ghent University as an extension of this descriptive monitoring.

My research project, funded by Ghent University, did not aim to evaluate management actions *senso stricto* but had the objective to document and predict variation in spider distribution in function of a changing landscape, where grazing is a tool to interconnect and enlarge the remaining grey dune fragments. Dispersal behaviour, a key element within spatial dynamics is therefore studied within an evolutionary-ecological context. Results of this study can be divided into two main sections: ***assemblage structure*** [chapters II.1-II.4] and the ***evolutionary ecology of spider dispersal*** [chapters III.1-III.8]. Both parts are introduced and discussed separately. A general discussion and conclusion can be found in chapter IV.1.

As this research project aims to address variation in distribution and dispersal in species from patchily distributed grey dunes, the assemblage structure of spiders from this habitat type is situated within the entire spider species composition of the coastal dune system in Flanders [***chapter II.2***] and indicator species and their level of specificity to this particular habitat type are analysed. Regional and local variation of spider assemblages from coastal grey dunes is investigated within a biogeographical and environmental framework in ***chapter II.3***. We especially focused on species distribution in relation to the geological [connectivity to other affiliated xerotherm habitats] and dynamical characteristics of the sampled regions and patches.

As dispersal is crucial in structuring species distribution, population structure and species ranges at large geographical scales or within local patchily distributed populations [Loreau & Mouquet 1999; Thomas & Kunin 1999], we present results on its evolutionary and ecological importance in part III of this thesis. As illustrated by Nathan [2001], the knowledge of dispersal evolution, motivation, its effect on metapopulation dynamics and species distribution at multiple scales is poorly understood and many questions remain unsolved or require empirical verification. In this part of the thesis we aim to contribute to the knowledge of dispersal, by studying both ecological and evolutionary aspects of spider dispersal in fragmented grey dunes. Studies were performed at the individual, population and assemblage level. Patterns of interspecific variation in ballooning dispersal and its effect on the species' distribution are documented in the ***chapters III.2 & III.3***. In the first, we address the relationship between habitat specialisation and ballooning dispersal propensity and hypothesised that specialised species can be expected to develop lower dispersal than generalists, as theoretically predicted by Kisdi *et al.* [2002]. These data on spider ballooning propensity were used to address the importance of ballooning dispersal versus the degree of habitat specialisation and the landscape configuration in shaping species distribution patterns [chapter III.3].

Because little is known on the possible relative contribution of prenatal environmental [maternal], genetic and postnatal environmental effects [different breeding conditions and acute starvation] on ballooning performance, we conducted a *G*enotype x *E*nvironment study on the money spider *Erigone atra*, which is characterised by a short generation time, easy breeding conditions and a well developed aerial dispersal [***Chapter III.4***].

In the three last chapters of part III, the contribution of both aerial and cursorial dispersal[1] in metapopulation dynamics of the dune wolf spider

Pardosa monticola and interdemic [and geographical] variation in both dispersal modes were studied within a fragmented dune landscape with patches of different quality. In ***chapter III.5***, we investigated general patterns in population dynamics of the dune wolf spider *P. monticola* and the relative importance of cursorial and aerial dispersal for patch colonisation and extinction. Population-genetical variation was additionally studied by allozyme electrophoresis. Because this model-approach only reveals general patterns and indirect evidence on the importance of dispersal, variation in aerial dispersal was studied more into detail in function of the landscape and the maternal habitat [***chapter III.6***]. Finally, emigration of *P. monticola* by means of cursorial dispersal was studied in three grasslands from different quality by pitfall trapping and by direct observations on orientation behaviour at different distances from the patch edge, within the moss-dune matrix [***chapter III.7***].

The following peer reviewed papers, often referred to in the text, but not included in this thesis can be downloaded from the website:

http://allserv.Ugent.be/~dbonte/pers/englishart.htm

Bonte, D., Hoffmann, M. & Maelfait, J.-P. 2000. Seasonal and diurnal migration patterns of the spider fauna of coastal grey dunes. *Ekologia* **19/4** suppl.: 5-16.

Bonte, D. & Maelfait, J.-P. 2001. Life history, habitat use and dispersal of a dune wolf spider [*Pardosa monticola* [CLERCK, 1757] Lycosidae, Araneae] in the Flemish coastal dunes [Belgium]. *Belgian Journal of Zoology* **131**: 141-153.

Bonte, D. & Mertens, J. 2003. The temporal and spatial relation between stenotopic dwarf spiders [Erigoninae: Araneae] and their prey [Isotomidae: Collembola] in coastal grey dunes: a numerical aggregative response or common microhabitat preference? *Netherlands Journal of Zoology* **52**: 243-253.

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1 *Dispersal by running*

Spiders as a model for bio-indication and the evolutionary ecology of dispersal

As taxonomic group, spiders are good candidates for bio-indication, because they form a species rich group, inhabiting all kinds of terrestrial ecosystems [Maelfait & Baert 1988a,b; Maelfait 1996; Marc *et al*. 1999; Maelfait *et al*., in press]. Additionally, each species has its own, well-documented, specific demands concerning humidity, temperature regime, litter and vegetation structure. This means that slight changes in habitat quality potentially cause significant changes in the composition of the spider assemblage. *Vice versa,* small changes in the spider composition of a habitat may indicate changes in the quality of that habitat. A practical reason to use spiders as bio-indicators, is that they are easy to sample in a standardised manner, at a relatively low cost [pitfall trapping]. Bio-indication at the level of the ecological assemblage can address differences in species diversity, species abundance, the occurrence of endangered species [Red list: Maelfait *et al*. 1998] and the functional group composition [Marc *et al*. 1999]. At the level of populations of individual species, bio-indication deals especially with evolutionary ecological aspects, in which interdemic variation[2] in life cycle patterns and other fitness related characteristics are addressed. More information on the use of spiders as bio-indicators of habitat quality and anthropogenic disturbance in Flanders is provided by Maelfait *et al*. [in press].

The availability of background information on habitat characteristics of spiders enables us to predict changes that can be adverted by management actions, their quick and fairly constant response towards [anthropogenic] stress and changes in the environment. Together with their easy standardised sampling, spiders meet the criteria of ecological indicators [*senso* Dale & Beyeler 2001]. Hence, spiders can be used as ecological indicators to assess the condition of the environment, to provide an early warning signal of changes in the environment, or to diagnose the cause of environmental problems and are useful for bio-indication.

Bio-indication at the population level is important within an evolutionary ecological framework and enables us to assess [often adaptive] variation in life-history traits in function of a changing environment, often induced by human activities. Illustrative is *e.g.* the evolutionary ecology of metal resistance in a wolf spider [see Hendrickx 2003] and the potential adaptive variation of reproductive output, age at maturity and dispersal propensity in function of quality and size of patchily distributed habitats. In this thesis, we focus on two different dispersal methods and how these are affected by habitat fragmentation and the related degradation of its quality. Spiders are good tools for evolutionary-ecological research of dispersal because phenotypic variation in both aerial and cursorial dispersal can be observed in the field. Also advantageous are the relatively simple standardised rearing conditions in many species and the directly measurable fitness component in species that guard or carry their eggsac. Interesting in studying aerial dispersal behaviour [ballooning] is the occurrence of behavioural adaptations in preparation of the ”flight” [tiptoe and dropping behaviour], which can easily be observed in a test chamber [see chapters III.1-III.8 of this thesis]. Based on behavioural observations, predictions can be made on the dispersal propensity of these species and the environment can be “manipulated” in the lab in order to study the potential evolutionary and ecological mechanisms acting on variation of this typical dispersal mode.

2 Variation between demes, here variation between populations

Grey dunes within a changing coastal dune ecosystem[3]

Grey dune, known as "*fixed coastal dunes with herbaceous vegetation*" includes Atlantic moss dominated dunes [mainly *Tortula ruralis*] as well as dune grassland [with a distinct organic soil layer] belonging to the *Cladonio-Koelerietalia* in case of lime rich grey dune and to the *Trifolio-Festucetalia ovinae* in case of decalcified grey dunes. The main differentiating processes are related to *dune fixation*, *soil formation* and *vegetation development*. These processes are closely interacting and each act within a specific spatiotemporal dimension [Provoost et al. 2002].

Dune fixation implies a decrease in aeolian activity and stabilisation by vegetation [Jungerius 1990]. Rhizome forming plants like *Ammophila arenaria* and *Festuca juncifolia*, which accumulate sand and persist only under aeolian dynamics, play an important part and are assumed to be an important nitrogen source in early stages of grey dune development [decaying material from tussocks of *Ammophila arenaria* for example]. This initial dune substrate is not very hospitable for plant growth. Drought stress is caused by climatological, geomorphological and pedological factors. Grey dune surface in Belgium, exposed to the sun can heat up to more than 60°C and soils can dry down to 20 cm deep [Aggenbach & Jalink 1999]. Additionally, the effect of water repellence, caused by soil organic matter, is an underestimated factor of drought [Ampe 1999]. This drought stress regime can strongly retard vegetation succession and soil development.

But even under these extremely harsh conditions, *biomass production* can take place at the early moss dune stages. This is the key element in soil development as humus colloids, produced by decomposition of organic matter, increase moisture retention and nutrient availability. Soil and vegetation processes are highly interwoven in the early stages of grey dune development and represent a classic example of internal succession according to the resource-ratio model [Tilman 1985]. This vegetation development occurs mainly in the rhizosphere and is driven by competition for water and nutrients. According to Slings [1994], grass roots are a main source of

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3 After Provoost et al. 2002 and Provoost, in press

4 Expansion of thick grassland vegetation, mainly Calamagrostis epigejos organic matter in grey dune soils. Veer & Kooijman [1997] found that root and moss biomass each are twice as large as the above ground vascular plant biomass, so probably mosses play an important role in further succession as well. Soil humidity is, however, the most important factor in biomass production and soil development.

Several processes counteract this humus accumulation. In young moss dunes, physical humus erosion can be substantial, but in stable grassland, main losses of soil organic matter are caused by biochemical decomposition. Bioturbation additionally enforces decomposition and mineralisation, as documented for ants [Dekoninck & Bonte 2002; Bonte *et al.* 2003e]. Stabilised dune soils decalcify due to continuous chalk leaching. At time of deposition, the sand is slightly calcareous [up to 8 % $CaCO_3$] thanks to shell fragments [Depuydt 1972]. During soil development, humic acids are released and enforce leaching of $CaCO_3$. Decarbonation of grey dune soils is again slowed down by mobilisation of calcareous sand, often after bioturbation. Weeda [1992] also considers 'sand spray', a slight sand accretion, as an important and characteristic natural cause of recalcification. According to the latter, this process prevents soil acidification and enhances decomposition and mineralisation of organic material in dune grasslands.

In natural dune systems, fine-scaled soil processes as mentioned above, physical destruction by blowing sand and [invertebrate] herbivory might be sufficient to preserve grey dune vegetation and its characteristic species, at least within an ephemeral pattern. But at present, substantial removal of plant biomass seems essential for sustainable dune grassland development. Coastal dune vegetation in Belgium and many other European countries evolve in one direction towards coarse grassland with *Calamagrostis epigejos*, *Avenula pubescens* or *Arrhenatherum elatius*, scrub with *Hippophae rhamnoides*, *Ligustrum vulgare* or *Salix repens* and woodland [van Til et al 2002, Provoost & Van Landuyt 2001]. Grass encroachment[4] is probably stimulated by atmospheric deposition but once established, grass dominated vegetation is highly self-maintaining due to an increased nitrogen mineralisation [Kooijman et al. 1998, Veer & Kooijman 1997]. Scrub expansion is mainly caused by drastic changes in land use. Up to the middle of the 20th century, livestock grazing was common in Belgian dunes and shrubs and trees were harvested for fuel. These activities kept the grey dune area far above the natural portion within the coastal ecosystem. Grazing and mowing can maintain vegetation structure and slows down [but does not stop] succession [De Raeve 1989]. Also, trampling and dung deposition, interact in the process of soil development. The natural processes described above can lead to moder humus, whereas in situations with livestock grazing a mullmoder humus is formed [Slings 1994, Aggenbach & Jalink 1999]. Grey dunes are as a result situated in the dry component of the ***stressed dune landscape***, where ecological dynamics are related to an equilibrium between top down regulating stress factors and bottom up organisation [xerosere vegetation development] [Fig. I.1]. They develop through succession and following fixation of habitats from the ***dynamic landscape*** [mobile and semi-mobile blond dunes] or by natural or human-induced [management] regression from habitats in the dry zone of the ***unconstrained landscape*** [shrub- and woodland].

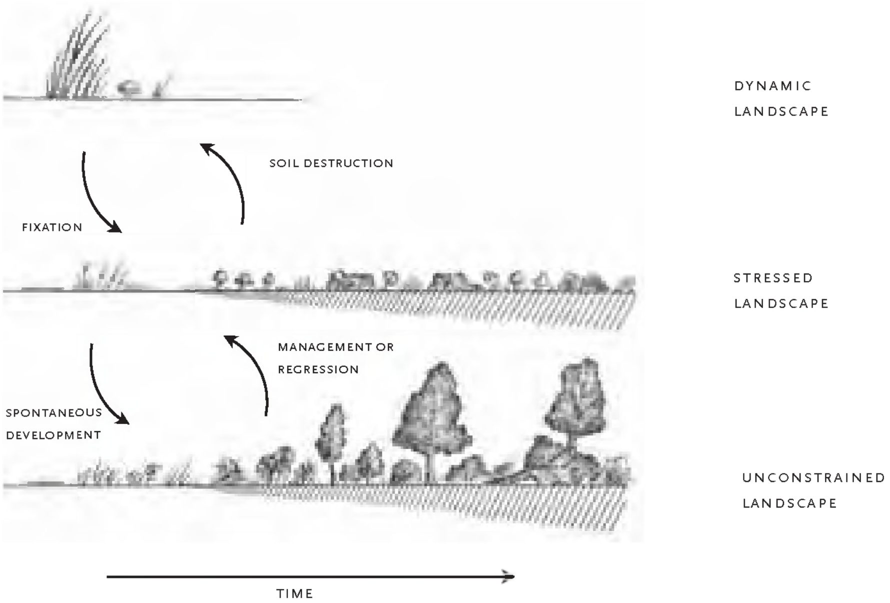

Fig. I.1: Schematic representation of the evolution of the three defined landscape types in the coastal dunes of Flanders and along the North Sea [Provoost et al. 2003]. Grey dunes are situated within the stressed landscape.

5 *Sand spray; Sand blowing dynamics*

At the landscape level, distribution of grey dunes is limited to dry or moderately moist zones within fixed dunes. As most of the dune ridges along the Flemish coast were still mobile some decades ago, only young moss dunes are found in these zones. Fixed dune grassland with a distinct soil profile is limited to intermediate elevations within large dune slacks or to relief-poor inner dunes. Stress factors form another determinant factor in grey dune distribution. Aeolic effects[5] for example, will only take place in the vicinity of mobile dunes. Herbivory pressure is related to rabbit density and present-day or historical livestock grazing. In Dutch dunes, an effect of agricultural activities related to sea villages is reflected in vegetation and species composition [Slings 1994] but this is not observed along the Belgian coast.

Along the western part of the Belgian coast, the grey dune area decreased from 730 to 350 ha since the fifties, mainly due to urbanisation and scrub encroachment. In addition, grey dunes are subject to internal degradation due to the grass encroachment mentioned above. Due to these elements, grey dunes occur patchily and have in general small areas. Until now, this evolution was not accompanied by a drastic decline in the total number of grey dune plant species. However, there is an apparent qualitative shift toward a less specific flora, amongst others because of garden escapes of exotic species [Provoost & Van Landuyt 2001]. In arthropods [grasshoppers *Oedipoda caerulescens, Stenobothrus stigmaticus*, butterflies *Hipparchia semele, Issoria lattonia,* digger wasp *Bembix rostrata* and spiders *Alopecosa fabrilis, Pardosa monticola, Xysticus sabulosus*] grey dune fragmentation influences patch occupancy patterns because of decreasing habitat quality and/or higher extinction dynamics without recurrent colonisation [Bonte & Maes, unpub. data; Bonte *et al*. 2003c]. These species, having different dispersal abilities, occur as a result in a patchy population structure [Hanski 1999] or a meta-population structure [Harrison 1991; Hanski 1999]. In patchily structured populations, individuals move freely among habitat patches, while in the second, most individuals stay in a single patch during their entire life, but dispersing individuals enhance strong colonisation-extinction dynamics. This results in a population structure in which suitable patches remain vacant. As shown for the dune wolf spider *Pardosa monticola*, occupancy patterns within metapopulation are often dependent on the size of the fragment [see chapter III.5; Fig. I.2].

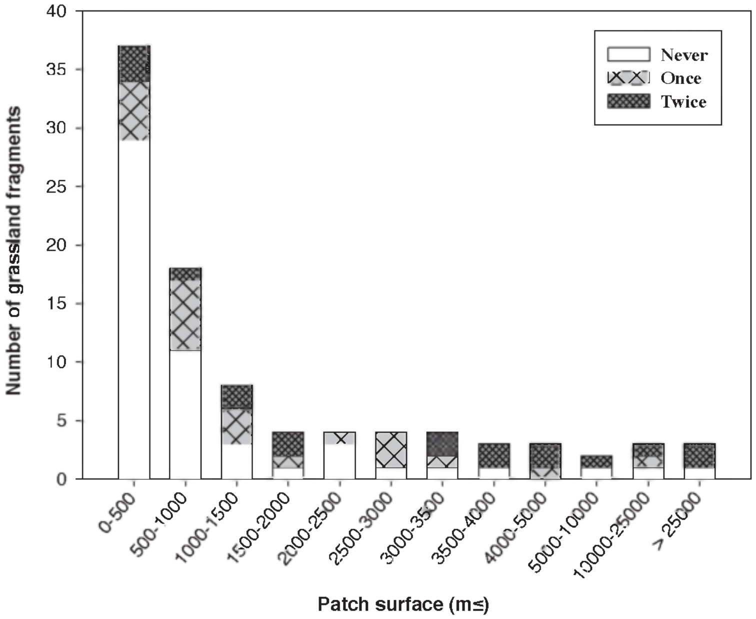

Fig. I.2: Patch occupancy frequency [never, once and twice occupied patches during two survey years] in the wolf spider Pardosa monticola in grey dune patches of different sizes.

This decline of at least regional biodiversity urges managers to take active nature management measures. Removal of scrub and woodland, mowing and grazing, have proven to be appropriate tools in dune grassland restoration. Well-documented examples of management schemes are available for the Dutch dunes [e.g. Annema & Jansen 1998] and the LIFE initiative at the Sefton coast in the UK [Houston et al. 2001]. In Belgian dunes, around 15 ha of scrub have been removed and currently nearly 350 ha are grazed [Herrier & Killemaes 1998a,b]. Mowing is only very locally used for grey dune management.

II.1

AN INTRODUCTION TO SPIDER ASSEMBLAGES OF COASTAL DUNES

FOTO: JOHAN DE MEESTER

Assemblages or communities are commonly used terms in defining patterns of co-existing species. A species community is composed of individuals, which interact in processes of mutualism, parasitism, predation and competition [Begon *et al*. 1996]. While community ecology mainly focuses on the way in which species are distributed in nature, the ways they are influenced by interactions and the physical focus of their environment, assemblages are more generally studied in order to describe species groups, occurring in different or similar habitats. Assemblages are as a result local snapshots of a spatiotemporal fluid system, having no status as distinct biological entities and hence dependent of species' life history patterns, dispersal capacities and environmental constraints [Hengeveld & Hemerik 2002].

The species' niche breadth is the most important property in structuring the assemblage. Hutchinson's niche theory, metapopulation theory and source-sink theory combined, provide a solid conceptual framework for the study of species distribution patterns [Pulliam 1988; Hanski 1998; Hanski 1999a,b; Pulliam 2000]. The empirical verification of this framework, however, remains surprisingly scant [Pulliam 2000] and species often prove absent from 'suitable habitat' [as predicted by the modified Hutchinson's *n*-dimensional niche concept; Hutchinson 1957] and present in 'less suitable' one [Pulliam 2000]. Species assemblages are hence not separated by clear and sharp boundaries, and do not exist as definable units, certainly not for mobile organisms in heterogeneous landscapes where edge effects enhance the occurrence of species outside their fundamental niche. Fundamental niches may even change in time, as shown for butterflies at expanding range margins if climatological conditions change [Thomas *et al*. 2001], due to a different response towards the use of resources. Species assemblages are as a result variable in space and time, but variation within the entire species assemblage and between defined groups can be studied by applying appropriate statistics.

According to Pianka [1994], patterns of species diversity and species composition can hypothetically be explained by various mechanisms, often functioning in a dependent way. The potential relevant mechanisms at the local scale of our study are:

- *Ecological time:* the time needed by a species to colonise newly opened or remotely areas of suitable habitat. Especially species characterised by poorly developed dispersal are expected to be absent in suitable habitat.

- *Spatial heterogeneity:* as the structural complexity of the habitat increases, the availability of microhabitats increases. Spatially heterogeneous habitats are hence expected to support more species than homogeneous ones.

- *Productivity*[6]*:* more productive habitats are characterised by a higher resource [prey] availability and hence allow greater dietary specialisation than do less productive habitats. Unproductive, but predictable habitats on the other hand can favour the presence of highly specialised species.

- *[Micro]climatic stability and predictability*: exploitation of environments with unstable and unpredictable climates often require that species have broad tolerance limits to cope with the wide range of environmental conditions they encounter. Stable and predictable habitats are expected to contain higher species diversity.

- *Disturbance*[7]: dependent on the magnitude of the disturbance, species assemblages can be over- or undersaturated. Diversity is enhanced by moderately frequent disturbances, but extremely frequent disturbances can dramatically reduce diversity, as predicted by the *Intermediate Disturbance Hypothesis*. Species, occurring in highly disturbed habitats will as a result be characterised by a broad niche spectrum [generalists] or a narrow niche breadth [specialists], linked to the mode of disturbance.

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[6] *The rate at which biomass is produced per unit area by plants [Begon et al. 1996]*

[7] *An event that removes organisms and opens space which can be colonised by individuals of the same or different species [Begon et al. 1996]*

Research on faunal species composition in the Flemish coastal dunes has already been performed on carabid beetles [Desender *et al.* 1992; Desender 1996], empidid and dolichopodid flies [Pollet & Grootaert 1996] and breeding birds [Bonte *et al.* 2001b]. Additional information on the biodiversity along the Flemish coast can be found in Provoost & Bonte [in press[a]]. In general, variation in species assemblages can be explained by variation in the vegetation structure or succession stage and humidity. Interesting, but largely unanswered questions are whether natural sand dynamics, one of the most typical abiotic characteristics of the Flemish coastal dunes, influence species distribution and how variation in species composition alters in function of an increasing fragmentation of the habitat. The increased fragmentation rate of grey dune and the accompanied reduction of its area, as a result of an increased urbanization and shrub encroachment [Herrier & Killemaes 1998a,b], is until now not accompanied by a drastic decline in the global number of grey dune plant species. However, there is an apparent qualitative shift toward a less specific flora, amongst others because of garden escapes of exotic species [Provoost & Van Landuyt 2001]. Typical grey dune butterflies have become extinct or very rare [Maes & Van Dyck 2001] and 95% of the typical dune carabid beetles are included in the Flemish Red List [Desender *et al.* 1995].

In contrast to higher plants [Stieperaere 1980], the Flemish coastal dunes are characterised by paucity of arthropod species, compared to inland xerotherm habitats and coastal dunes in the neighbouring countries [Maelfait *et al.* 2000; Zegers 2001; Bonte *et al.* 2002c]. This lower species richness is believed to result from the typical young and dynamic landscape development. We can hence expect that species have experienced difficulties in colonising the coastal region of Flanders, and that environmental dynamics have enhanced continuous extinction processes, in which species were unable to survive. This in contrast to many higher plant species, which are able to survive unsuitable conditions in time by persistent seed banks [Murren *et al.* 2001]. Dispersal abilities in space and time are hence potential determinants of species assemblages in the Flemish coastal dunes.

In **chapter II.2**, we analyse the structure of the spider assemblage in the Flemish coastal dunes. The analysis is based on data from more than 170 pitfall year-round sampling campaigns from the 1970s onwards performed by scientists at Ghent University, the Institute of Nature Conservation [Brussels] and the Royal Belgian Institute of Natural Sciences [Brussels]. As grey dunes, a vegetation type characterized by a xerotherm species composition, are extremely fragmented since the second half of the 20th century, species composition was investigated more in detail in function of the patch size.

The spider assemblages of these grey dunes were additionally compared to those from the Boulonnais-region and the Netherlands [**chapter II.3**]. Since grey dune habitats in these regions are located in older dune landscapes, which are connected to structurally similar habitats [respectively chalk grasslands and heathland], we hypothesised that differences in species richness could be attributed to connectivity and the age of the landscape. We also addressed whether coastal aeolian dynamics, absent in the Netherlands dune region, influence the species composition of grey dunes.

II.2 SPIDER ASSEMBLAGE STRUCTURE AND STABILITY IN A HETEROGENEOUS COASTAL DUNE SYSTEM [BELGIUM]

FOTO: DRIES BONTE

Bonte D., Baert L. & Maelfait J.-P. 2002. Journal of Arachnology 30: 331-343

Abstract

An analysis of the spider assemblage structure and the presence of indicator species in the Flemish coastal dunes is presented. The analysis is based on data from more than 170 pitfall year-round sampling campaigns from the 1970s onwards. We were able to find indicator species for almost all identified habitats. The assemblages are structured by variation in vegetation structure [succession], atmospheric and soil humidity and the presence of both natural and anthropogenic disturbance. In the fragmented habitats [grasslands and grey dunes], a clear relationship was found between the mean habitat size and the stability of the assemblage composition. More detailed studies on the species-area relationship of spiders in moss dominated dunes and short grasslands indicated that total species numbers do not increase as a function of the patch size. The total number of typical species is, however, higher in larger patches. These results indicate higher edge influences in small patches and the importance of microhabitat variation [which should be higher in large patches], or, minimal population size for the presence of characteristic species in these habitat patches.

Keywords: Araneae, indicator species, habitat size, species-area relationship

Introduction

Coastal dunes in Europe have been the subject of several spider species composition studies and revealed that the species composition is very typical due to the presence of many rare and threatened species. Especially in Northern [Almquist 1973] and Western Europe [Duffey 1968; Bell *et al*. 1998], studies have been conducted. Carabid beetle [Desender *et al*. 1992; Desender, 1996], and dolichopodid flies [Pollet & Grootaert 1996] have also been studied in the Flemish coastal dunes. This kind of general information is necessary for the assessment of the conservation value of habitats in Flanders and Europe. General assemblage descriptions together with more detailed knowledge of landscape-level ecological relationships such as multi-habitat use [Bonte *et al*. 2000a], colonization abilities [Bonte *et al*. 1998], population genetics [Desender *et al*. 1998], population dynamics [Desender 1996; Baert & Desender 1993], minimal population sizes and population structure should be integrated in nature conservation policy.

Since the beginning of the 20th century the total area of unbuilt coastal dunes in Flanders [Belgium] diminished from approximately 6000 ha to less than 3800 ha [Vermeersch 1986]. The Flemish dunes are characterised by an overall increase of competitive plant species like Sea Buckthorn *Hippophae rhamnoides,* Burnet Rose *Rosa pimpinellifolia* and Wood Small Reed *Calamagrostis epigejos*, due to the retreat of local dune farmers after WW II and a decrease of the rabbit population due to myxomatosis and VHS viral diseases. This shrub and grass encroachment is possibly triggered by atmospheric N-deposition and enhanced by positive feedbacks in the nitrogen cycle [Veer 1997] by the increasing coverage of nitrogen-fixating Sea Buckthorn. The soil nitrogen and mineral content will influence the trophic status of the vegetation, which is strongly related to the amount of organic components in the upper soil layer [Krabbenborg *et al*. 1983] Current habitat management is directed to the conservation and restoration of wet, herbaceous grasslands in dune valleys and stable mesophytic grasslands through large-scale removal of shrub, followed by grazing by domestic horses and cattle. In this contribution, we will first define the indicator spider species for all of the dune habitats by the analysis of pitfall-data as a tool for future monitoring and investigate which parameters influence the variation in species composition. Since a crucial question in habitat restoration is the effect of patch area on the presence of typical species [stenotopic species], the species-area relationships for two fragmented habitat types are additionally investigated.

Methods

Data collection

The total assemblage analysis is based on data from more than 178 pitfalls, which were linearly placed in all kinds of dune habitats in the Flemish coastal dunes during an entire year, from the 1970s onwards [Hublé 1975; Hublé 1976; Van Biervliet 1978; Hublé & Maelfait 1981; Baert & Desender 1993; Maelfait 1993; Bonte & Hendrickx 1997; Bonte *et al*. 1999; Baert *et al*., unpub. data]. In each sampling station [row of pitfall traps within one habitat], three to five traps were regularly placed, with a distance of 5-10 meter between each pitfall [the traps are glass jam jars with a diameter of 9.5 cm, filled with a 10% formaline solution]. All dune habitat types were sampled since 1975 and in total more than 65000 adult spiders were identified, resulting in data on the presence of 214 different species. Voucher specimens are deposited at the Royal Belgian Institute of Natural Sciences in Brussels. Of these, 159 species were caught with more than five individuals and can thus be considered as resident species and not as rare vagrants [cfr. Maelfait & Baert 1988a]. The sampled vegetation types, the dominant plant species and the number of used pitfall traps are listed in Table II.2-1.

Community structure and Indicator species

The community-structure is indirectly determined via Detrended Correspondence Analysis [Hill 1979a] with the data from the separate pitfalls. Only the more abundant species were taken into account for the ordination analysis. This methodology reveals a multidimensional ordering of the samples [here traps] based on their species composition similarity in

Type	**Indicative plant species**	**number of pitfall-traps**
Dune woodland	Trees : *Alnus glutinosa, Acer pseudoplatanus*	3
High, woody shrubs	Shrubs: *Crataegus monogyna, Hippophae rhamnoides*	13
Thick humid Calamagrostis grasland	Grass: *Calamagrostis epigejos*	20
Vital humid Sea-buckthorn-Liguster scrubs	Shrubs : *Hippophae rhamnoides, Salix repens, Ligustrum vulgare*	10
Wet eutrophic open dune valleys	Sedges and grasses: *Juncus subnodulosus, Carex riparia, Iris psudacorus*	6
Thick dry *Arrhenatereum* grassland	Grasses: *Arrhenatherium elatius, Avenula pubescens*	13
Dry Sea buckthorn shrub [in grassland mosaics]	Shrub: *Hippophae rhamnoides*	6
Dwarf scrubs	Dwarf-shrub: *Rosa pimpinellifolia*	18
Wet mesotrophic open dune valleys	Sedges and grasses: *Juncus subnodulosus, Carex trinervis, C. flacca*	12
Short grazed mesophytic grasslands	Grasses and herbs: *Luzula campestris, Galium verum, Avenula pubescens, Koeleria albescens*	15
Wet oligotrophic dune valleys	Grasses and sedges: *Juncus articulatus, Carex trinervis*	10
Marram dunes	Grass: *Ammophila arenaria*	9
Moss dominated dry oligotrophic dunes [Grey dunes]	Mosses, annual herbs and grasses: *Tortula ruralis ruraliformis, Aira praecox, Erodium cicutarium, Corynephorus canescens*	29
Bare sand dunes	grass: *Festuca rubra arenaria*	9
Anthropogenic disturbed sand dunes	herb: *Cirsium arvense*	5

Table II.2-1 - **Characterisation and total number of pitfall-data from the sampled dune habitats** which traps with a similar assemblage are closely ordered, while those with a completely different species composition are order distantly. Since habitat characteristics were never studied in a standardized way during the several sampling campaigns, only the habitat type and the linked biotic and abiotic variables were indirectly used for the analysis of the parameters structuring the spider assemblage. Data on stage in vegetation succession, depth of the groundwater level and different kinds of disturbance were taken from Provoost & Hoffmann [1996]. Different kinds of disturbance result from natural aeolic dynamics [sand overblowing] and anthropogenic factors due to different intensive nature management techniques like mowing of the vegetation [once or twice a year] and grazing [year-round] for the conservation of oligo- and mesotrophic pastures.

We used a TWINSPAN-clustering [Hill 1979b] for the determination of the different levels of assemblage similarity, based on the species composition from each pitfall trap. In this way a hierarchical ordering is obtained, in which samples are dichotomous separated at different levels. The separation at the first level splits the samples in two different and large groups with common species. The samples from both groups are then again separated based on differences in their species composition. The total dataset is in this way dichotomous clustered in five levels, where the highest levels represent the most detailed sample separation.

Indicator species for all groups at the different levels from the TWINSPAN-classification were determined with the Indval-method [Dufrêne & Legendre 1997]. With this methodology, an indicator value is calculated for a species in each cluster group. The indicator value is calculated as

$\mathrm{IndVal}_{ij}=A_{ij} * B_{ij} * 100$, where $A_{ij} = \mathrm{Nindividuals}_{ij}/\mathrm{Nindividuals}_{i}$ and $B_{ij}=\mathrm{Ntraps}_{ij}/\mathrm{Nsites}_{j}$.

In this formula A_{ij} is a measure of group specificity, where $\mathrm{Nindividuals}_{ij}$ is the mean number of individuals of species i across traps of group j and $\mathrm{Nindividuals}_{i}$ is the sum of the mean numbers of individuals of species i over all groups at that level. B_{ij} is a measure of fidelity, where Ntraps_{ij} is the number of traps in group j where species i is present, while Nsites_{j} is the total number of traps in that group. A_{ij} is maximum when species i is only present in group j, while B_{ij} is maximum when species i is present in all traps of the group j. A random reallocation procedure of traps among groups is used to test the significance of INDVAL [500 permutations]. This index [INDVAL] is thus maximal when all individuals of a species are found in a single group of traps and when the species occurs in all traps of the group. As a consequence the maximal indicator value can be interpreted as a measure for habitat specificity.

Because pitfall data record [species specific] activities instead of absolute densities, we only analysed our data by presence/absence in the ordination, clustering and IndVal calculation. In this way, bias to different climatological conditions between years could be eliminated.

Assemblage stability and species-area relationships

The mean Euclidean distance between the different axes scores for pitfalls from the same assemblage, as derived from the multi-dimensional DCA-ordination, were used as a measure for the assemblage instability. Low Euclidean distances characterize traps that sampled analogue species composition, while traps with a completely different species should have a high Euclidean distance [are ordered distantly]. This distance measure is thus an indication for the species composition similarity between traps from the same assemblage. High similarities result thus in low distances and indicate stabile species assemblages.

Due to shrub- and grass encroachment mesophytic short grasslands and humid valley habitats became fragmented and decreased in surface. A decrease of the surface can influence the assemblage structure: especially for small habitat patches, the assemblage stability should decrease because of the extinction of species and the presence of typical species from adjacent habitats. Therefore, we related the habitat [in]stability to the average surface of the different fragmented habitat types as derived from digitised vegetation maps [Provoost & Bonte, unpub. data]. Differences in stability between assemblage groups were assessed with Analysis of Variance and elated to habitat areas with Spearman correlations.

For moss dominates dunes and short mesophytic grasslands [for which we have exact surface data], we also determined the relation between the total number of species and the number of indicator species, trapped in three pitfalls, and the surface of the sampled grassland patch. This species-area relationship was correlatively studied with Pearson correlations for all species and for all the indicator species in function of the area of the sampled habitat patch, separately for moss dominated dunes and short dune grasslands.

Results

Assemblage structure

A total of 15 spider assemblages were characterized by the TWINSPAN clustering. The first division clearly separates the eutrophic vegetations from the meso- and oligotrophic, short grazed habitats. The eutrophic assemblages are separated at the lowest level in dune woodlands, shrubs, marshland and dense grasslands. The mesotrophic and oligotrophic habitats are separated within the second group [Fig.II.2-1] in short, rabbit-grazed grasslands, mown mesotrophic dune valleys, moss dominated dunes, dynamic Marram-grass [*Ammophila arenaria*] dominated dunes and bare dunes. Significant indicator species per cluster group [Monte Carlo permutations; 500 runs] and their indicator value are listed in Table II.2-2.

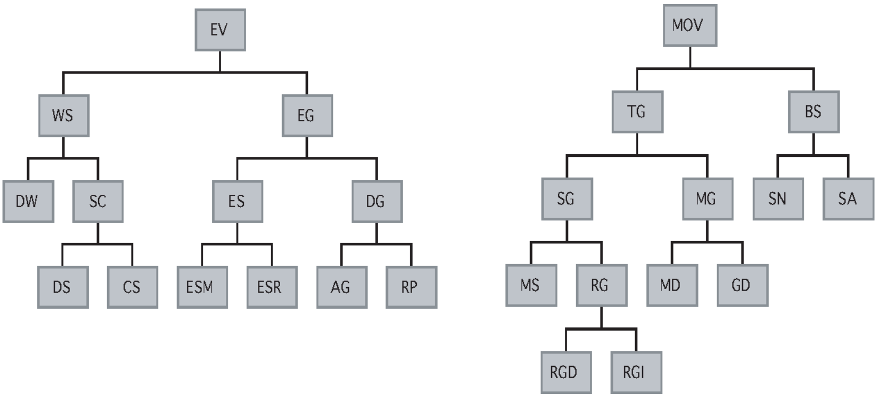

Fig.II.2-1: Dichotomous TWINSPAN clustering of the spider composition, based on the species presence/absence data [abbreviations for the assemblages: see Table II.2-2]

The ordination-analysis clearly visualizes the assemblage structure along three relevant axes. The first axis [eigenvalue 0.689] separates the different samples along a vegetation structure-gradient, where dune woodlands are plotted on the left, bare sandy habitats on the right. The second axis [eigenvalue 0.587] separates the humid from the dry habitats: dune valley vegetations [dune slacks] and Marram dunes above and moss dominated dunes [grey dunes] below [Fig.II.2-2]. Interesting is the higher position along the second axis of Marram dunes near the seaside in comparison with those from the inner dune front. This stresses the importance of atmospheric humidity in addition to soil humidity as the second important assemblage structuring parameter. The third relevant axis [eigenvalue 0.383; Fig.II.2-2] is associated with natural [wind in Marram dunes, inundations in dune slacks] and anthropogenic dynamics [especially habitat management: mowing & grazing in short grazed pastures and dune slack meadows], which are all ordered in the lower part of the ordination.

Table II.2-2 - Indicator species [Monte Carlo permutations, P<0.01] and indicator value [IndVal] at the different cluster levels [See Fig.II.2-1], with description of the assemblage habitat characteristics

Habitat [Abbreviation] and habitat characteristics	Indicator species	IndVal
Eutrophic vegetation [EV]	*Alopecosa pulverulenta* [Clerck, 1757] [Lycosidae]	74.97
High, litter rich, dense	*Bathyphantes parvulus* [Westring, 1851] [Linyphiidae]	51.04
Dry or humid	*Centromerus prudens* [O.P.-Cambridge, 1873] [Linyphiidae]	60.06
	Centromerus sylvaticus [Blackwall, 1841] [Linyphiidae]	87.08
	Clubiona comta C.L. Koch, 1839 [Clubionidae]	23.60
	Clubiona lutescens Westring, 1851 [Clubionidae]	25.71
	Episinus angulatus [Blackwall, 1836] [Theridiidae]	16.85
	Ero furcata [Villers, 1789] [Mimetidae]	47.03
	Euryopus flavomaculata [C.L. Koch, 1836] [Theridiidae]	49.49
	Floronia bucculenta [Clerck, 1757] [Linyphiidae]	27.77
	Gonatium rubens [Blackwall, 1833] [Linyphiidae]	69.57
	Linyphia triangularis [Clerck, 1757] [Linyphiidae]	12.94
	Maso sundevalli [Westring, 1851] [Linyphiidae]	43.76
	Meioneta saxatilis [Blackwall, 1844] [Linyphiidae]	46.09
	Neriene clathrata [Sundevall, 1830] [Linyphiidae]	25.97
	Ozyptila simplex [O.P.-Cambridge, 1862] [Thomisidae]	71.09
	Palliduphantes ericaeus [Blackwall, 1853] [Linyphiidae]	19.97
	Palliduphantes pallidus [O.P.-Cambridge, 1871] [Linyphiidae]	69.56

Habitat [Abbreviation] and habitat characteristics	**Indicator species**	**IndVal**
	Pirata hygrophillus Thorell, 1872 [Lycosidae]	49.16
	Pocadicnemis juncea Locket & Millidge, 1953 [Linyphiidae]	59.63
	Robertus lividus [Blackwall, 1836] [Theridiidae]	74.39
	Theridion bimaculatum [Linnaeus, 1758] [Theridiidae]	33.35
	Trochosa terricola Thorell, 1856 [Lycosidae]	88.01
	Walckenaeria acuminata Blackwall, 1833 [Linyphiidae]	47.11
	Walckenaeria atrotibialis [O.P.-Cambridge, 1878] [Linyphiidae]	93.17
	Zora spinimana [Sundevall, 1833] [Zoridae]	66.94
Meso- oligotrophic vegetation [MOV] Short, sparse vegetation Rabbit grazed Dry or humid Sandy patches	*Arctosa perita* [Latreille, 1799] [Lycosidae]	63.24
	Haplodrassus dalmatensis [L. Koch, 1866] [Gnaphosidae]	73.01
	Meioneta rurestris [C.L. Koch, 1836] [Linyphiidae]	34.49
	Parapelecopsis nemorals [O.P.-Cambridge, 1884] [Linyphiidae]	53.85
	Styloctetor romanus [O.P.-Cambridge, 1872] [Linyphiidae]	37.22
	Tegenaria agrestis [Walckenaer, 1802] [Agelenidae]	24.72
	Xysticus sabulosus [Hahn, 1832] [Thomisidae]	40.28
Woodland and woody shrubs [WS] High vegetation and litter rich Presence of trees [*Crataegus monogyna*]	*Tapinopa longidens* [Wider, 1834] [Linyphiidae]	19.35
	Walckenaeria nudipalpis [Westring, 1851] [Linyphiidae]	44.13
Dense grasslands [EG] Dense and tall grass layer Litter-rich Dry or humid	*Clubiona diversa* O.P.-Cambridge, 1862 [Clubionidae]	8.09
	Cnephalocotes obscurus [Blackwall, 1834] [Linyphiidae]	35.07
	Enoplognatha thoracica [Hahn, 1833] [Theridiidae]	30.89
	Ero cambridgei Kulczynski, 1911 [Mimetidae]	11.53
	Pachygnatha degeeri Sundevall, 1830 [Tetragnathidae]	71.92
	Pisaura mirabilis [Clerck, 1757] [Pisauridae]	18.92
	Walckenanaeria antica [Wider, 1834] [Linyphiidae]	41.61
Thermophilious grasslands [TG] Short, no or scarce litter Dry or humid Dynamics: wind, grazing or mowing	*Agroeca lusatica* [L. Koch, 1875] [Liocranidae]	37.57
	Alopecosa barbipes [Sundevall, 1833] [Lycosidae]	34.59
	Bolyphantes luteolus [Blackwall, 1833] [Linyphiidae]	16.00
	Centromerita concinna [Thorell, 1875] [Linyphiidae]	62.25
	Walckenaeria monoceros [Wider, 1834] [Linyphiidae]	32.82
	Xysticus kochi Thorell 1872 [Thomisidae]	64.91

Habitat [Abbreviation] and habitat characteristics	**Indicator species**	**IndVal**
Bare sand [BS]	*Erigone longipalpis* [Sundevall, 1830] [Linyphiidae]	57.14
No vegetation		
Dune woodland [DW]	*Ceratinella scabrosa* [O.P.-Cambridge, 1863] [Linyphiidae]	43.48
Dominance of trees		
[*Alnus glutinosa*]	*Diplocephalus picinus* [Blackwall, 1841] [Linyphiidae]	82.86
Litter-rich	*Enoplognatha ovata* [Clerck, 1757] [Theridiidae]	14.29
Humid	*Macrargus rufus* [Wider, 1830] [Linyphiidae]	19.05
	Pardosa saltans Töpfer-Hofmann, 2000 [Lycosidae]	66.67
	Tapinocyba insecta [L. Koch, 1869] [Linyphiidae]	56.60
	Tenuiphantes zimmermanni [Betkau, 1890] [Linyphiidae]	85.19
Woody shrubs [SC]	*Monocephalus fuscipes* [Blackwall, 1836] [Linyphiidae]	88.92
Dominance of Sea Buckthorn [*Hippophae rhamnoides*]		
and *Calamagrostis epigejos*		
Presence of trees		
[*Crataegus monogyna*]	*Saaristoa abnormis* [Blackwall, 1841] [Linyphiidae]	44.44
Eutrophic wet dune valleys [ES]	*Centromerita bicolour* [Blackwall, 1833] [Linyphiidae]	42.17
Humid, Winter inundations	*Ceratinella brevipes* [Westring, 1851] [Linyphiidae]	29.78
High, dense vegetation	*Clubiona reclusa* O.P.-Cambridge, 1863 [Clubionidae]	34.38
Dominance of *Carex riparia*	*Dicymbium nigrum* [Blackwall, 1834] [Linyphiidae]	63.62
	Gnathonarium dentatum [Wider, 1834] [Linyphiidae]	15.63
	Pachygnatha clercki Sundevall, 1823 [Tetragnathidae]	50.86
	Pardosa palustris [Linnaeus, 1758] [Lycosidae]	83.92
	Pardosa pullata [Clerck, 1757] [Lycosidae]	71.79
	Pirata latitans [Blackwall, 1849] [Lycosidae]	85.49
	Pirata piraticus [Clerck, 1757] [Lycosidae]	42.19
	Tiso vagans [Blackwall, 1834] [Linyphiidae]	71.12
	Troxochrus cirrifrons [O.P.-Cambridge, 1871] [Linyphiidae]	30.95
	Troxochrus scabrosa [Westring, 1851] [Linyphiidae]	34.57
Short mesotrophic grasslands [SG]	*Pardosa monticola* [Clerck, 1757] [Lycosidae]	53.43
Dry or humid [winter indundations]		
Marram and moss dominated dunes [MG]	*Agroeca cuprea* Menge, 1873 [Liocranidae]	66.98
Sandy, scarce vegetation	*Drassodes cupreus* [Blackwall, 1834] [Gnaphosidae]	50.05
Mainly mosses and lichens	*Dysdera crocata* C.L. Koch, 1838 [Dysderidae]	17.81
Ammophila arenaria- tussocks	*Metopobactrus prominulus* [O.P.-Cambridge, 1872] [Linyphiidae]	37.83
	Poeciloneta variegata [Blackwall, 1841] [Linyphiidae]	15.79
	Sitticus saltator [O.P.-Cambridge, 1868] [Salticidae]	32.50
	Thanatus striatus C.L. Koch, 1845 [Thomisidae]	39.97

Habitat [Abbreviation] and habitat characteristics	**Indicator species**	**IndVal**
Antropogenic disturbed sandy soils		
[SA]	*Pardosa proxima* [C.L. Koch, 1847] [Lycosidae]	57.14
Bare sand, human activities		
Dense shrubs [DS]	Agyneta subtilis [O.P.-Cambridge, 1847] [Linyphiidae]	29.70
Dominance of *Hippophae*		
rhamnoides and *Ligustrum vulgare*	*Gongylidium rufipes* [Linnaeus, 1758] [Linyphiidae]	61.78
	Microneta varia [Blackwall, 1841] [Linyphiidae]	24.48
	Ozyptila praticola [C.L. Koch, 1837] [Thomisidae]	31.43
	Pholcomma gibbum [Westring, 1851] [Theridiidae]	11.54
	Walckenaeria cucculata [C.L. Koch, 1836] [Linyphiidae]	43.50
Degradating Shrub [CS]	*Agyneta decora* [O.P.-Cambridge, 1871] [Linyphiidae]	10.77
Shrub with open patches, colonised		
by *Calamagrostis epigejos*	*Ceratinella brevis* [Wider, 1834] [Linyphiidae]	22.00
Humid	*Kaestneria pullata* [O.P.-Cambridge, 1863] [Linyphiidae]	41.95
Wet rough litter rich vegetation		
[ESR]	*Clubiona phragmites* C.L. Koch, 1843 [Clubionidae]	35.71
Rough, eutrophic vegetation		
Inundations, no management	*Xysticus ulmi* [Hahn, 1831] [Thomisidae]	16.67
Dry dense grasslands-shrub mosaics		
[AG]	*Agyneta conigera* [O.P.-Cambridge, 1863] [Linyphiidae]	11.48
Mosaics of low shrubs and		
Avenula-grassland	*Hahnia nava* [Blackwall, 1841] [Hahniidae]	31.79
Dry, no management	*Metellina mengei* [Blackwall, 1870] [Tetragnathidae]	14.29
	Maso gallicus Simon, 1894 [Linyphiidae]	20.21
	Philodromus cespitum [Walckenaer, 1802]	17.54
High dwarf shrubs [RP]	*Alopecosa cuneata* [Clerck, 1757] [Lycosidae]	28.18
Dominance of *Rosa pimpinellifolia*		
and *Arrhenaterium elatius*	*Heliophanus flavipes* [Hahn, 1832] [Salticidae]	26.67
High grass layer	*Xysticus erraticus* [Blackwall, 1834] [Thomisidae]	36.42
Presence of litter	*Trachyzelotes pedestris* [C.L. Koch, 1837] [Gnaphosidae]	27.78
Mesotrophic dune valleys [MS]	*Arctosa leopardus* [Sundevall, 1833] [Lycosidae]	33.79
Dominance of *Juncus subnodulosus*	*Clubiona trivialis* C.L. Koch, 1843 [Clubionidae]	36.11
Yearly mowed	*Collinsia innerans* [O.P.-Cambridge, 1885] [Linyphiidae]	20.00
Winter inundations	*Erigone arctica* [White, 1852] [Linyphiidae]	65.51
	Erigone promiscua [O.P.-Cambridge, 1873] [Linyphiidae]	74.74
	Prinerigone vagans [Audouin, 1826] [Linyphiidae]	56.45

Habitat [Abbreviation] and habitat characteristics	**Indicator species**	**IndVal**
	Gongylidiellum vivum [O.P.-Cambridge, 1875] [Linyphiidae]	39.46
	Oedothorax apicatus [Blackwall, 1850] [Linyphiidae]	41.59
	Oedothorax fuscus [Blackwall, 1834] [Linyphiidae]	74.22
	Oedothorax retusus [Westring, 1851] [Linyphiidae]	58.23
Short Mesoptrophic grasslands		
[RG]	*Thyphochrestus digitatus* [O.P.-Cambridge, 1872] [Linyphiidae]	42.21
wet [inundating] or dry, rabbit grazed		
Marram dunes [MD]	*Clubiona frisia* Wunderlich & Schuett, 1995 [Clubionidae]	75.41
Dominance of Marram grass		
[*Ammophila arenaria*]	*Clubiona subtilis* L. Koch 1867 [Clubionidae]	31.07
Strong wind dynamics, close to		
the sea	*Micaria pulicaria* [Sundevall, 1831] [Gnaphosidae]	55.56
Scarce vegetation	*Porrhomma microphthalmum* [O.P.-Cambridge, 1871] [Linyphiidae]	14.81
	Tibellus maritimus [Menge, 1875] [Thomisidae]	18.52
	Trochosa ruricola [De Geer, 1778] [Lycosidae]	28.70
Moss dominated dunes & Marram dunes near the inner dune front		
[GD]	*Alopecosa fabrilis* [Clerck, 1757] [Lycosidae]	20.85
Dominance of lichens and mosses	*Micaria dives* [Lucas, 1846] [Gnaphosidae]	18.97
Scarce Marram grass vegetation	*Walckenaeria stylifrons* [O.P.-Cambridge, 1875] [Linyphiidae]	30.38
Near inner dune front	*Zelotes longipes* [L. Koch, 1866] [Gnaphosidae]	66.70
Dry mesotropic grasslands [RGD]	*Pelecopsis parallella* [Wider, 1834] [Linyphiidae]	35.81
Rabbit grazed, short grass layer		
Dominance of *Luzula campestris*	*Trichopterna cito* [O.P.-Cambridge, 1872] [Linyphiidae]	45.98
Inundating mesotrophic grasslands		
[RGI]	*Cheiracanthium virescens* [Sundevall, 1833] [Clubionidae]	51.43
Inundating, short Carex-vegetation	*Lepthothrix hardyi* [Blackwall, 1850] [Linyphiidae]	26.98
Presence of Creeping willow		
[*Salix repens*]	*Xerolycosa miniata* [C.L. Koch, 1834] [Lycosidae]	64.55

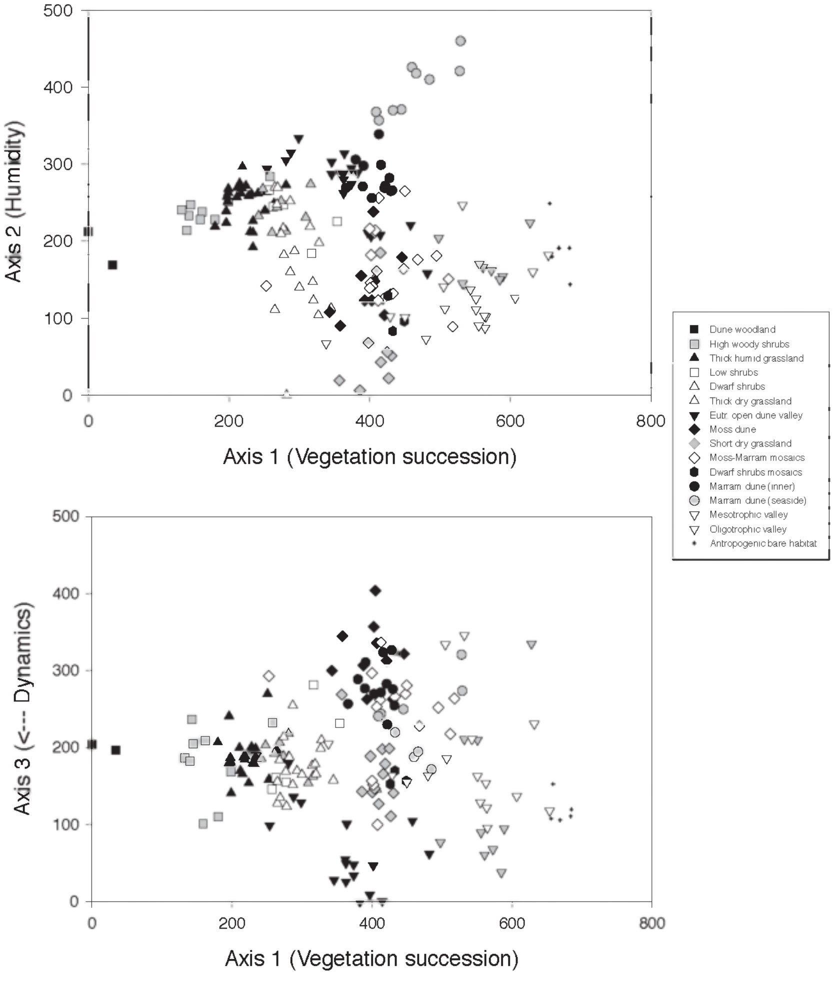

Fig.II.2-2: DCA-ordination of the pitfall data, based on the species abscence/presence data, with indication of the habitat type. Above: ordination along the first and the second axis; below: ordination along the first and the third axis

Stability of assemblages from oligo- and mesotrophic habitats and species-area relationships

The assemblage stability differs between the different distinguished spider assemblages from oligo- and mesotrophic habitats [Bare sand [BS], mown eutrophic valleys [ESM], Moss dominated dunes [GD], Marram dunes [MD], Mesophytic dune slacks [MS], Dry mestrophic grasslands [RGD] and inundating mesotrophic grasslands [RGI] [one way-ANOVA, $F_{1,6}$=11.403, P<0.001]. The stability is significantly different between the assemblage groups BS, ESM, GD, MD and the assemblages of MS, RGI, RGD, but doesn't differ within the two groups. Correlation with average patch size is nearly significant [Spearman R=-0.750, P=0.052] and indicates that assemblages from small habitats tend to be more diverse in species composition. The species-area relationship of the total number of species and the total number of specific [indicator] species in function of the area of moss dominated dune and short dune grassland patches is illustrated in Fig.II.2-3. The relation between patch size and total number of species is not significant for either the moss dominated or the short dune grasslands [Fig.II.2-4: Pearson correlation, r=0.20; P>0.05]. The number of resident indicator species however is higher in large patches in both vegetation types [Fig.II.2-4: Pearson correlation for moss dunes: r=0.87, P<0.01 and for dry mesoptrophic dune grasslands: r=0.93, P<0.01].

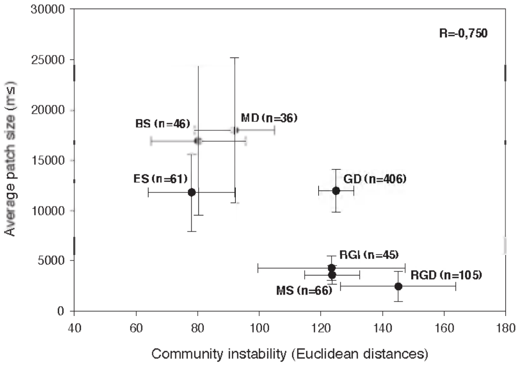

Fig.II.2-3: Assemblage instability of fragmented grassland and dune valley habitats [mean Euclidean distance of DCA scores and 95% confidence intervals; n=number of distance measurements] in function to the average habitat patch size [means and 95% confidence intervals]. Abbreviations see Table II.2-2

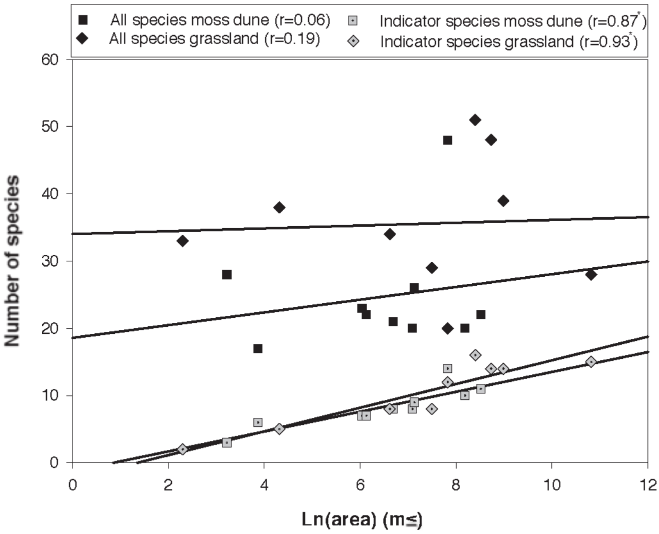

Fig.II.2-4: Species-area relationship for all species and indicator species caught on moss dominated dry dunes and short grasslands from different sizes [Spearman correlation, *: P<0.01].

Discussion

Our results indicate that almost all dune system habitat types are characterized by the presence of indicator species, dependent on the cluster level. Desender [1996] demonstrated within this framework that typical dune species show strong year-to-year fluctuation in their population size [or trapping efficiency]. This variation could largely be explained by variation in climatological variables. We believe that the fact that samples were taken in different years is an advantage for the identification of indicator-species based on the IndicatorValue method, since in this way turn-over events due to different meteorological conditions, which result in the extinction of typical species [as demonstrated by Baert & Desender 1993; Gajdos & Toft 2000], are negligible. We used even only absence/presence data, so true indicators that are always present [independent of their yearly activity] are unambiguously identified, while difference in activities [and thus absolute trapping numbers] is neglected.

Besides year-to-year fluctuations, species assemblages can vary as a function of habitat conditions and landscape structure. Our analysis is based on an extended data set from habitats of different size and from different landscape configurations, so the determined indicator species can be used as bio-indicators for future monitoring of the conducted nature management in both open [dominance of grasslands, Marram dunes] and [shrub dominated] closed dune landscapes.

That fact that the variation in species assemblages can be explained by variation in the vegetation structure or succession stage is not surprising and has been documented several times in other studies on invertebrate assemblages [spiders: Duffey 1968; Almquist 1973, carabid beetles: Desender *et al.* 1992; Empidid and dolichopdid flies: Pollet & Grootaert 1996]. Our study indicates the importance of atmospheric and soil humidity as a second important assemblage structuring component, since wet vegetation types are clearly separated from dry ones, and Marram dunes near the sea-side were separated from those of drier more inland dunes. Indicative for the importance of atmospheric humidity is the presence of species from dune valleys [*Clubiona frisia* and *C. subtilis*] in Marram dunes near the seaside are, while they are completely absent from the same habitat near the inner dune front [1-2 km from the seaside], where atmospheric humidity is significantly lower [Provoost & Hoffmann 1996]. The same phenomenon [defined as double ecological occurrence] has also been documented by Duffey [1968] in British coastal dunes. A third important abiotic source of variation is defined here as habitat disturbance. The third axis separates stable habitats without disturbance [woodland, shrubs, dwarf shrubs, rough permanent grasslands] from habitats with high natural disturbance [inundations: wet open dune slacks; aeolic dynamics: Marram dunes, bare dunes] and anthropogenic disturbance [grazing and mowing management]. These habitats are characterized by ruderal species like *Erigone atra, E. dentipalpis, E. arctica, Oedothorax fuscus, O. retusus, O. apicatus* and *Bathyphantes gracilis* which are all short-living, have a rapid juvenile development and a well-developed ballooning dispersal capacity.

This data analysis is based only on the presence of adult spiders. Earlier studies have indicated that species typical for open habitats like short grasslands and moss dominated dry dunes [grey dunes] need proximate patches of dense and litter-rich vegetation for their juvenile development and/or retreat during unfavourable periods in their mature life-stage [Bonte *et al*. 2000a,b]. Thus, habitat variation can strongly alter the presence of spider species bound to these dense vegetation patches for their juvenile development. Although not documented for spider populations, a minimal patch area can determine the presence of viable population size [1999a]. In both cases, an increasing patch area should affect the spider assemblage directly because patch area influences the population size or indirectly because an increasing patch size enhances internal microhabitat variation. Our results on the assemblage level show that the stability of spider assemblages in patchy habitats depends on the mean patch area, indicating that differences in the spider assemblage vary more in natural small habitats than in larger ones. Edge effects in small habitats can alter the spider assemblage dramatically, because of a higher presence of typical species out of the surrounding vegetation. This is certainly true for moss dominated dunes and short grasslands: total species numbers do not differ in function of the patch size while the number of indicator species significantly increases with an increasing patch size. An explanation of this species-area relationship cannot be given without further research on both internal niche heterogeneity and minimal population sizes. Especially variation in soil conditions can explain the aggregation of soil-dwelling arthropods like springtails *Collembola* [Bonte & Mertens, unpub. data]. Since these are the main prey for typical juvenile wolf spiders and adult dwarf spiders, a larger patch size can alter the total number of indicator species indirectly by the presence of a higher internal niche variation. For the study of minimal patch size and related population size, more detailed studies are however needed on meta-population dynamics, based on the survey of a higher number of habitat patches.

II.3 Regional and local variation of spider assemblages [Araneae] from coastal grey dunes along the North Sea


FOTO: DRIES BONTE

Bonte D., Criel P., Van Thournout I. & Maelfait J.-P. 2003. *Journal of Biogeography* 30: 901-911

Abstract

This study aims to determine the underlying causes of local and regional patterns of variation in spider assemblages from coastal grey dunes, especially whether ecological time constrains the species composition in young and isolated grey dunes habitats. The study was conducted in coastal dunes from Northern France [Boulonnais, Nord-Pas-de-Calais], Belgium [Flemish coastal dunes] and the Netherlands [Amsterdam Water Supply dunes and Dunes from the Provincial Water Company North-Holland]. Spiders were collected with pitfall traps in 28 grey dune patches in the four investigated areas. Species composition and environmental parameters [vegetation structure, distance to the sea and the patch-edge, aeolic dynamics, lime richness] were determined. Assemblage composition was related to the regional and local environmental factors with the Primer software package to determine the assemblage-determining parameters. Differences in species presence were analysed in function of their habitat preference and distribution range.

Differences in grey dune spider assemblage structure can mainly be attributed to differences in local sand dynamics and the region. Species from dynamic dunes are mainly present in grey dunes from Belgium and France, while species from non-dunal xerothermic habitats [chalk grasslands and heathland] occur in both the Boulonnais and the North Holland dune region. These species are absent from geologically young habitats and from the Flemish coastal dunes, which are isolated from other xerotherm habitats. Our data show that regional variation in spider assemblage composition results from local landscape characteristics [dynamics in the dune area], the latitude and the connectivity to non-dunal xerothermic habitats. The strong and moderate geological isolation of dune areas from respectively the Flemish coast and the Amsterdam Water Supply dunes results in the absence of [at least some] species that are primarily bound to heathland and/or chalk grassland. This indicates the importance of ecological time for the assemblage structure. The limited dispersal capacity of the absent species is probably the major reason for this paucity.

Keywords: biogeography, xerotherm species, sand dynamics, heathland, chalk grassland

Introduction

Grey dune, known as "Fixed coastal dunes with herbaceous vegetation" in the CORINE biotope classification [Natura 2000], is most readily defined using plant species composition. Vegetation includes Atlantic moss dominated dunes [mainly *Tortula ruralis*] as well as dune grassland [with a distinct organic soil layer] belonging to the *Cladonio-Koelerietalia* assemblage in case of lime rich grey dune and to the *Trifolio-Festucetalia ovinae* assemblage in case of decalcified grey dunes [Provoost *et al.* 2002]. Ecologically, grey dunes can be defined simply as the dry component of the "stressed" dune landscape, where ecological dynamics are controlled by climatological stress and xerosere progression. The main differentiating processes are related to dune fixation, soil formation and vegetation development [Provoost & Hoffmann 1996; Aggenbach & Jalink 1999].

Grey dune succession is initiated by fixation of sand by mainly *Carex arenaria* roots and driven by the complex of soil formation [humus accumulation] and vegetation development. Leaching and mobilisation of $CaCO_3$ complicate the picture and are important in nutrient dynamics. But at present, rough grass- and scrub encroachment greatly overrule these fine-scaled soil processes and cause substantial loss of regional biodiversity [Provoost *et al.* 2002]. Due to this encroachment, grey dunes are now heavily fragmented and patchily distributed within a matrix of dense dune vegetation [shrubs, dense grassland]. In an earlier paper, we already identified typical species for this habitat [Bonte *et al.* 2002a] and found that this habitat type is characterised by a specific and endangered arthropod fauna [Bonte *et al.* 2002d]

Assemblages are local snapshots of a spatiotemporal fluid system, having no status as distinct biological entities and hence dependent of species' life history patterns, dispersal capacities and environmental constraints [Hengeveld & Hemerik 2002]. Dispersal and geographical factors together determine the ecological time necessary to enable potential species for establishment [Pianka 1994]. The structure of spider assemblages in European coastal dunes is at this moment well documented [Bøggild 1961; Duffey 1968; Almquist 1973; Noordam 1996; Bonte *et al.* 2000b; Gajdos & Toft 2002; Bonte *et al.* 2002a] and characterised by geographical and temporal variation. Locally, assemblages are mainly structured by the vegetation development, the soil- and aerial humidity. Some authors also stressed the importance of sand dynamics as an important structuring parameter [Gajdos & Toft 2002; Bonte *et al.* 2002a]. Whether differences in species composition, or more specifically the absence of apparently good adapted species, is the result of insufficient ecological time to colonise young and isolated dune areas is at this moment unclear. This factor is certainly thought to be one of the causes of the general species paucity of the Flemish coastal dunes, compared to those more located inland [Maelfait *et al.* 2000]. Within this geological young and relatively strong isolated dune region [Declerck & De Moor 1996], grey dune habitats are even younger because of their successive character [Provoost *et al.* 2002] and more isolated because large dune regions are only interconnected by beach.

Grey dune vegetation has high affinities with heathland and chalk grassland vegetation [Weeda *et al.* 1996] and possess a lot of common species. Therefore, we tested the hypothesis that ecological time can constrain the species composition from the young an isolated grey dunes in the Flemish coastal dunes by comparing its spider species composition [from which habitat characteristics are well documented in Western and Middle Europe [Hänggi *et al.* 1995]] and assemblage structure to those from the Boulonnais area in Northern France, which is directly connected to chalk grasslands and the Netherlands which are directly or historically connected to heathland. Evidently, ecological time had to be discriminated from local and regional environmental variation.

Material and methods

Study area

The investigations were conducted in four dune regions along the coasts from Northern France, Belgium and the Netherlands [Fig.II.3-1]. The dune area in the Boulonnais region [Northern France, Department Nord-Pas de Calais; approximately 4000 ha] is situated in and connected to a basin of lime formations of the cuesta from the Haut-Boulonnais [De Meuter *et al.* 1982; Colbeaux 1985]. The oldest parts of the coastal dunes [Pré Communal d'Ambleteuse] were formed during the Flandrian regression [5000 BC] on a fossil lime formation. The more recent coastal dunes [from 2000 BC onwards] are situated at the seaside of the lime cuesta and consist of lime-rich sands [Antrop & Verhoeve 1980; Bellenfant *et al.* 1998].

The Flemish coastal dunes [approximately 3000 ha] in the most Northern part of France and the west coast of Belgium originated partly before [2000-3000 BC] and after the Romanian period [300-800 AC]. They are situated on marine clay sediments and isolated from older [inland] sand- or lime depositions [Declerck & De Moor 1996]. The coastal dunes of the Amsterdam Water Supply [AWD; 3400 ha] are situated in the provinces of South- and North-Holland, in the Netherlands and belong to the dunes of the Renodunaal district. The old dunes were formed on old sandy beaches, which originated 3000 BC. From the Romanian period onwards, dune formation continued and the young dunes were formed in front of the old dunes. The lime content of the sands is high [Baeyens & Duyve 1992; Ehrenburg 1994]. The dunes of the Provincial Water Company North-Holland [PWN; 5800 ha] originated at the same period as the AWD and are situated at the borderline between the Renodunaal district with lime rich sands and the Waddendistrict, which are completely decalcified [Klijn, 1981]. This differentiation is the result from two different sea currents, which meet each other near Bergen aan Zee [Klijn 1981]. In the North [North European dunes, included the Wadden district], sand depositions are initially low in lime and nutrients, compared to those in the south [south European dunes, included the Renodunaal district].

As a result of their geological history, grey dunes from the Boulonnais region make contact with chalk grassland on the Cretacious questa, while those in the PWN are connected with well-developed dune heathlands from the Wadden district. The dune area of the AWD is historically connected to the Wadden district, but nowadays isolated due to urbanisation; the Flemish coastal dunes are completely isolated from other xerotherm habitats.

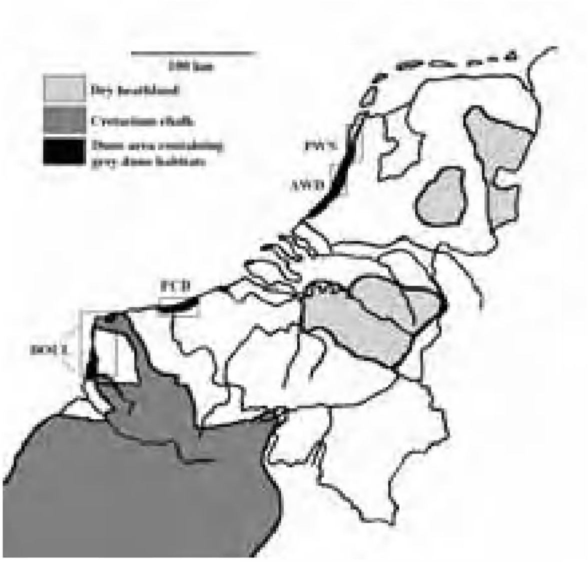

Fig.II.3-1: Location of the four sampled dune regions and the presence of suitable geological conditions for the presence of dry heathland and Cretaceous chalk grasslands in Northern France, Belgium and the Netherlands.

Sampling methodology and the determination of the environmental parameters

In each region, we selected relatively large grey dune remnants [Bonte *et al.* 2002a found that the richness of specific species declined in small patches] in order to sample the maximal amount of regional variation in an equal way. Seven sites were sampled in the Boulonnais and the Flemish coastal dunes, six in AWD and eight in PWN. Additionally, well-developed heathland [two sites in PWN] and chalk grassland [two sites in the Boulonnais] were sampled in order to determine the presence and the abundance of possible dune-invading species. In each station, five pitfall traps [diameter of nine centimetre, filled with a 6% formaline-detergent solution] were linearly installed, with an inter-trap distance of five meters [due to vandalism, only data from three traps could be used from one station in the Boulonnais and the AWD]. The sampling took place in the period March-November 1999 and traps were fortnightly emptied.

Around each pitfall, we determined the vegetation composition by applying the Londo-scale [Londo 1975] for the cover of the dominant plant species and the cover of non-overgrown mosses, herbs and bare sand. Additionally, we measured the soil development [depth of the humus-rich A-horizont] and the height of the vegetation to the nearest cm. Thirty measurements were taken from the vegetation height with a polystyrene plate [diameter 20 cm], placed on a measuring rule. The standard deviation was determined as a measure for the variation in vegetation height. Since it is correlated with the vegetation height [r_{132}=0.867; P<0.001], the ratio SD/mean height was used as an independent parameter. The distance to the nearest dense vegetation was measured in the field; the distance to the sea was derived from terrain maps.

Additional environmental data were inferred from Aggenbach & Jalink [1999], who linked the presence and cover of indicator plant species to the following soil parameters in a ranked quantitative way: nutrient availability, lime content, aeolian value [ranked severeness of sand overblowing] and humus development. The estimate for humus development was almost perfectly correlated with our measurements made on soil development and was replaced by the latter in this study [r_{132}= 0.834; P<0.001]. It also stresses the reliability of the inferred parameters. All the determined environmental parameters are listed in Table II.3-1. Because of the possibility of covariation, these environmental parameters were analysed for principal components by PCA-analysis. In case of significant correlation along the principal axes, component scores were used as a new environmental parameter. All environmental parameters were averaged for each site.

Parameters	PCAnutrient		KW- Region	
	r 132,PCA1	P	H[3,28]	P
Distance to the sea [m]	-0.033	NS	0.139	NS
Mean vegetation height [cm]	0.375	<0,001	--	--
Variation in vegetation height [SD/mean height]	-0.164	NS	4,827	NS
Cover herbs and grasses [%]	0.400	<0,001	--	--
Cover non-overgrown mosses [%]	-0.365	<0,001	--	--
Cover bare sand [%]	-0.246	<0.01	5,946	NS
Distance to the edge - dense vegetation [m]	0.054	NS	0.593	NS
Depth of A-horizont [cm]	0.409	<0,001	--	--
Aeolian value	-0.278	<0.01	0.670	NS
Lime content value	0.006	NS	2,598	NS
Nutrient availability value	0.371	<0,001	--	--
PCAnutrient	--	--	4,757	NS

Table II.3-1- Pearson correlations of the determined environmental parameters with the first and only significant principal component and results of the Kruskal-Wallis ANOVA of the remaining environmental parameters with region as factor. —: Not relevant

Main habitat of the species

The main habitat of the species was derived from Hänggi *et al.* [1995], Roberts [1998], Maelfait *et al.* [1998], Bonte *et al.* [2002a] and Nentwig *et al.* [2002]. Additional sampling occurred in dune heathland and chalk grassland in respectively the PWN and Boulonnais area [Bonte 1999; Bonte *et al.* 2001a]. In this way, species could be categorized as eurytopic or stenotopic for dynamic coastal dunes, for xerotherm habitats [coastal and inland dunes and a variety of oligotrophic dry grasslands], heathland, chalk grassland or for both heathland and chalk grassland. Finally, southern and northern-limited species were identified [species respectively at the northern and southern limit of their distribution range].

Data analysis

Pitfall traps register arthropod activity patterns, and are affected by both the population density and the species-specific movement rates [Maelfait &

Baert 1975]. As a result, they are biased by inter- and intraspecific activity variation due to different climate and population characteristics. Therefore, presence-absence data are used instead of the relative or absolute numbers.

As a consequence, data are binomial distributed and classical [canonical] correlation based multivariate ordination techniques cannot be used for analysis. The use of PRIMER [Clarke & Ainsworth 1993] is however an elegant and extremely suitable alternative. By applying this algorithm, a dissimilarity Bray-Curtis matrix of the species data [most common species, at least caught in five individuals in one site] is compared by rank correlation with a Euclidian similarity matrix of all possible combinations [subsets] of environmental data [n! combinations; n=number of environmental parameters]. The best subset of environmental variables that provides the best match between the two configurations reveals hence the 'best explanation' of the biotic structure, analogue to a forward multiple regressions. All the determined environmental parameters and the region, ranked by latitude were included in the environmental dataset.

We visualised the dissimilarity between the sites by non-metric multi dimensional scaling [NMDS, with indication of the stress value as an indication for the stability of the ordination] and the Bray-Curtis dissimilarity tree.

An earlier analysis [Bonte *et al.*, in press] revealed that the total number of caught species increases with the amount of sampled sites [and traps], but that >95% of all specific xerotherm species from one region are caught with 25 pitfall traps, distributed over a variety of grey dunes. Locally, all specific species are caught with 3 to 5 traps. As a consequence, absolute counts were used to compare diversity of specific species between regions.

The proportions of all present species, belonging to the determined habitat categories, were compared between the four dune areas with multiple c^2-comparisons and post-hoc Tukey tests [Zar 1996]. Basic statistical tests [Kruskal-Wallis ANOVA; correlations] were conducted with Statistica 5.5 [Statsoft 2000]; Principal Component Analysis with PCORD 4.17 [McCune & Mefford 1999].

Results

Local and regional environmental variation of the sampled grey dune habitats

The PCA-analysis revealed only one significant principal component, which explained 34.642 % of the total variation [eigenvalue = 4.503 > broken stick eigenvalue = 3.180]. This principal component was significantly correlated and explained more than 10% covariation with the mean vegetation height, the cover of the grass/herb layer and the moss layer, the depth of the A-horizont and the nutrient availability [Table II.3-1]. Although other significant relationships exist, we consider them as ecologically independent because of the low amount [<10%] of explained covariation. In summary, the principal component reflects variation in nutrient availability, resulting in a higher cover and height of grasses, herbs, a deeper soil development and a lower cover of non-overgrown mosses. In further analyses, we will refer to this principal component as $PCA_{nutrient}$.

The values of the final seven independent environmental parameters do not differ between the four regions [Kruskal-Wallis ANOVA; H[3,28]; Table II.3-1], so differences in spider species composition and diversity cannot be attributed to differences in environmental conditions of the sampled sites between the four regions.

k	Best variable combination [R]
1	Aeolics [0.488]
2	Aeolics x Region [0.550]
3	Aeolics x Region x Bare sand [0.643]
4	Aeolics x Region x Bare sand x PCAnutrients [0.584]
5	Aeolics x Region x Bare sand x PCAnutrients x distance to the sea [0.560]
6	Aeolics x Region x Bare sand x PCAnutrients x distance to the sea x Variation vegetation height [0.510]
7	Aeolics x Region x Bare sand x PCAnutrients x distance to the sea x Variation vegetation height x Lime value [0.438]
8	All parameters [0.388]

Table II.3-2 - Combination of variables, k at time, giving the largest rank correlation between biotic [spider presence/absence] and environmental similarity matrices. In bold: final subset of parameters, explaining the largest amount of assemblage variation.

Local and regional variation in spider assemblage structure

The variation in spider assemblage structure is primarily determined by differences in the aeolian value and the region. Thirdly, the cover of bare sand is an important assemblage-structuring factor. Variation in aeolic dynamics explains 23.81 % of the assemblage variation. The amount of explained variation is increased with 6.44% when region is included. The combination of the three parameters results in the best subset, explaining in total 41.34% of the assemblage variation. If more parameters are included, the explaining power decreases significantly [Table II.3-2]. The NMDS ordination of the sites, based on the species presence-absence records indicates the same pattern of the assemblage composition: although no differences between the environmental parameters were recorded [Table II.3-2], the regions are differentiated along the first NMDS-axis [Kruskal-Wallis ANOVA; H[3,28]=15.312, P=0.002] but not along the second one [Kruskal-Wallis ANOVA; H[3,28]=7.461 , P=0.059] [Fig.II.3-2]. Spearman correlation of the first NMDS axis indicates that this differentiation is only the result of differentiation in the aeolian value [R_{28}=-0.525; P=0.004] and the $PCA_{nutrient}$-scores [R_{28}=0.603; P<0.001]. No linear relationships along the second axis were found.

The Bray-Curtis dissimilarity tree also reveals the existence of five distinct groups: all the sites of the Netherlands [I] and one partial group of the Boulonnais [IIa] and the Flemish Coastal dunes [IIIa] are separated from two other groups [sites with aeolic dynamics] from the latter regions [IIb and IIIb] [Fig.II.3-2].

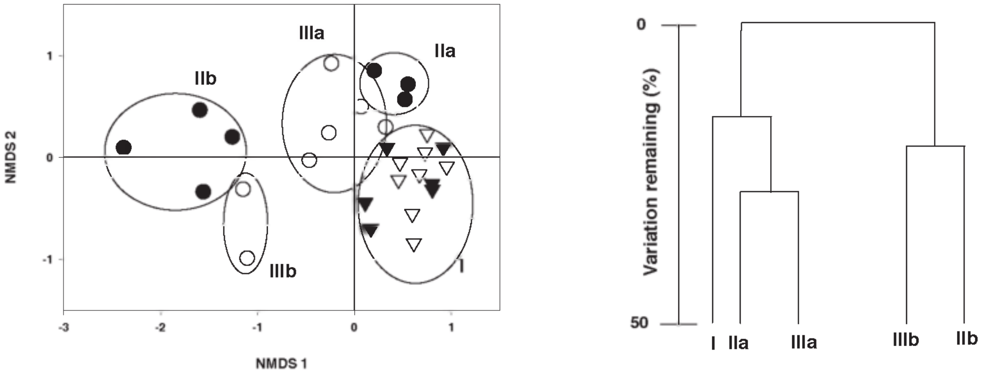

Fig.II.3-2: NMDS-ordination [left] and Bray Curtis dissimilarity tree [right, branches of the sites belonging the same group are merged] of the sites, based on the absence-presence of the spider species. Filled circles: Boulonnais region [IIa,b]; Open circles: Flemish coastal dunes [IIIa,b]; Filled triangles: Amsterdam Water Supply dunes [I]; Open triangles: Dunes North-Holland PWN [I]

Regional variation in species richness

The number of eurytopic species is significantly different between the four regions [χ^2=17.901; n_{tot}=130; P<0.001] and is highest in PWN [n=88], moderate in FCD [n=70] and BOUL [n=71] and lowest in AWD [n=53]. The number of widespread xerotherm species is however not significantly different in the four regions [n_{tot}=31; n_{Boul}=27; n_{FCD}=30; n_{AWD}=27; n_{PWN}=28; χ^2=2.298; P>0.05].

The number of species from dynamic coastal dunes is higher in the Boulonnais and the Flemish coastal dunes than in the dunes from the Netherlands [χ^2=11.917; n_{tot}=7; P<0.001; Fig.II.3-3a] and occur in high abundances [Appendix 1]. Southern species are mainly present in the Boulonnais dune area [χ^2=25.567; n_{tot}=11; P<0.001; Fig.II.3-3b]. Only one Northern-continental species was recorded in the coastal dunes of the Netherlands [*Centromerus incilium*].

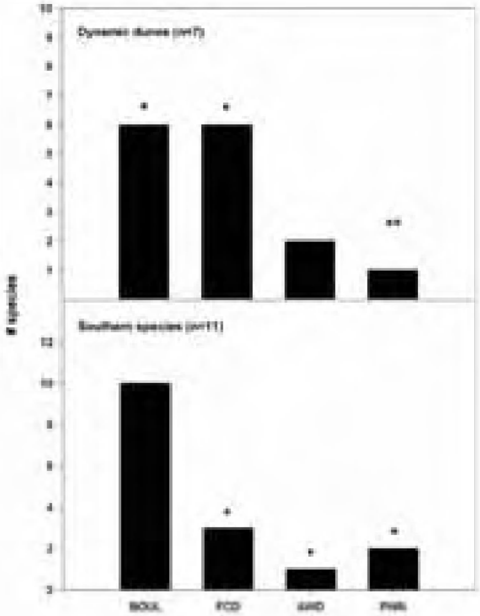

Fig.II.3-3: The number of typical dynamic dune species [3a, above] and Southern species [3b, under] in the four investigated dune regions. Bars indicated with the same symbol indicate non-significant differences [Tukey-test; P>0.05]. boul: Boulonnais; fcd: Flemish coastal dunes; awd: Amsterdam Water Supply dunes; pwn: Dunes Provincial Water Company North-Holland

Typical species for chalk grasslands are only present in the Boulonnais dunes [Fig.II.3-4a]. Heathland species are only present in the coastal dunes of the Netherlands and more numerous in the dune area of PWN [Yates corrected $\chi^2=8.423$; $P<0.01$], than in AWD [Fig. II.3-4b]. Species, which have their optimum in both habitat types, are equally present in the dunes of the Boulonnais, AWD and PWN. Only the Flemish coastal dunes are characterised by an almost completely absence of these species [$\chi^2=22.209$; $n_{tot}=17$; $P<0.001$; Fig. II.3-4c]. For all these xerotherm species together, the deficit in the Flemish coastal dunes is even more pronounced [$\chi^2=45.998$; $n_{tot}=34$; $P<0.001$]. The number of species, belonging to this lumped category, is higher in the AWD than in the Flemish coastal dunes but significantly lower than in the dune area of the PWN and the Boulonnais.

Of these, the heathland species *Cercidia prominens, Textrix denticulata* and *Zelotes subterraneus*, the chalk grassland species *Hypsosinga pygmaea, Walckenaeria furcillata, Dysdera erythrina, Euophrys herbigrada* and *Steatoda* *albomaculata* and four species typical for both habitats [*Cheiracanthium erraticum, Haplodrassus umbratillis, Micrargus subaequalis, Araeoncus humilis*], are only encountered in very low numbers in the coastal grey dunes [Appendix 1]. The other non-typical dune species were abundant and some of them also occurred in the more isolated, though historically connected, dune area of AWD.

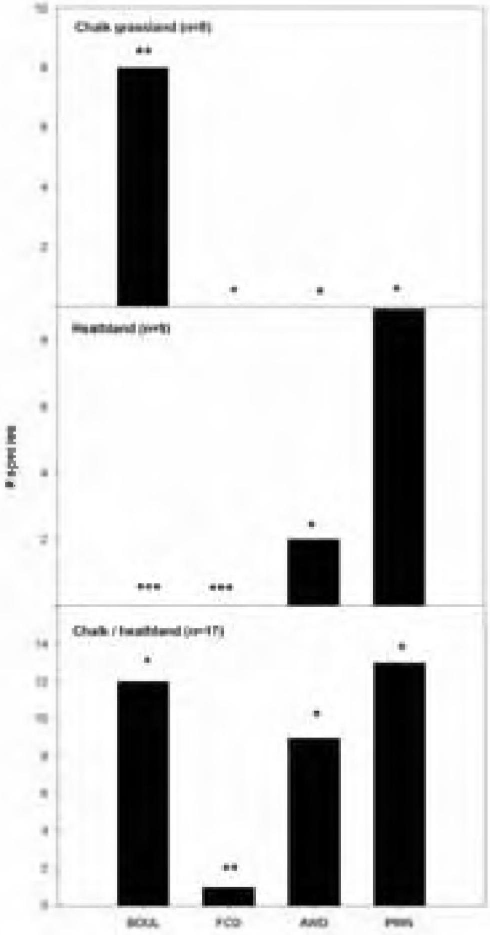

Fig.II.3-4: The number of stenotopic xerotherm species in the four investigated dune regions. Bars indicated with the same symbol indicate non-significant differences [Tukey-test; P>0.05]. 4a[above]: chalk grassland species; 4b [middle]: heathland species; 4c [below]: species typical for heathland and chalk grassland. boul: Boulonnais; fcd: Flemish coastal dunes; awd: Amsterdam Water Supply dunes; pwn: Dunes Provincial Water Company North-Holland

Discussion

Our results show that spider assemblage structure and species richness in the four large dune regions along the North Sea of Northern France, Belgium and the Netherlands are region specific and locally determined by variation in sand dynamics. Species from dynamic coastal dunes are present in the Flemish coastal dunes and Northern France, but absent from the Netherlands although environmental variation in the sampled patches was not different. Species with optima in chalk grassland and heathland were only present in respectively grey dunes from the Boulonnais and the North-Holland dune region, directly connected to the former xerotherm habitats. These species were absent from the isolated and geological young Flemish coastal dunes and in a lesser amount present in the dunes of the Amsterdam Water Supply dunes, which are distantly and historically connected to dune heathland. Regional variation in spider assemblage structure and species richness can hence be attributed to general landscape and ecological time constrains [time needed for species to colonise distant and young suitable habitats].

Spider and arthropod communities in coastal dunes are in general structured by gradients in vegetation development and both soil and aerial humidity [Duffey 1968; Van der Aart 1970; Almquist 1973; Koehler *et al*. 1995; Desender 1996; Pollet & Grootaert 1996; Bell *et al*. 1998; Mattoni *et al*. 2000]. Bonte *et al*. [2002a] also found that dynamics due to sand displacement and nature management act as a determining factor for the assemblage composition. In this contribution however, we only investigated the variability in spider species composition of one habitat type [grey dunes] in the mainland coastal dunes along the North Sea. The most important spider assemblage determining factors in these grey dunes are again related to sand dynamics. In grey dunes from the four regions, the two most important assemblage determinants are after all the aeolian value [a measure of the degree and severeness of sand overblowing] and the cover of bare sand, which should not a priori be related to the former parameter since f.i. trampling and digging activities significantly affect the presence of nude sand on grey dunes, especially at places with a young soil development.

Spider assemblages are however not uniformly and geographically structured, a pattern also observed in inland dunes from the German lowlands [Merkens 2002]. A first interesting result from our study is the separation of the Netherlands coastal dunes from those investigated along the Belgian and Northern French coasts. Although no environmental differences in the studied sites were found, coastal dunes of the Netherlands were characterised by species from nutrient rich vegetation and by the absence of species from dynamic dune systems. This indicates that although local habitats are suitable, other factors influence the observed pattern. As found by Mattoni *et al.* [2000] historical disturbance can alter the species richness of dune arthropods in a definitive way. We believe that the absence of these typical coastal dune species originates from the global dune landscape structure: in contrast to the coastal dunes from Northern France and Belgium, large-scale fixation of dynamic sand dunes started in the 16th century and was very stringent in the 19th and the 20th century [Klijn 1981], as a human response to the strong maritime inundation which affected large parts of the Netherlands. Nowadays, cattle graze in these coastal dunes and sand dynamics are again tolerated [Anonymus 1992; Hillen & Roelse 1995; Janssen 1995; van Boxel *et al.* 1997]. Although habitat restoration took place very quickly, the spider assemblage reacts apparently slowly and still lacks typical coastal dune species in comparison to comparable grey dune habitats along the Belgian and Northern French coast.

An earlier analysis of the spider diversity in the Flemish coastal dunes indicated that the number of possibly encountered eurytopic species increases with the amount of sampled sites and the amount of used pitfall traps, but that almost all xerotherm species are caught with a limited amount of traps [Bonte *et al.*, in press]. This biologically means that an increasing sampling effort results in a higher chance in finding non-typical species, invading from other surrounding dune habitats but that no typical species will be caught additionally. This sampling bias hence explains the high amount of eurytopic species in the regions that were intensively sampled. Of more interest is the increased richness of non-dunal xerotherm species in these regions that are directly connected to heathland and chalk grassland and the paucity in the isolated Flemish coastal dunes. The increased diversity in grey dune habitats, connected to other xerotherm habitats, originates most likely from two different processes: [i] non-typical xerotherm species invade the grey dune from the adjacent optimal habitats in a source-sink system [Hanski 1999a] or [ii] non-typical xerotherm species have established populations in the neighbouring coastal grey dunes but limited dispersal capacities and the lack of time enabled them to spread to more distant and/or geological younger regions. For species with only marginal population sizes, grey dune habitats function as sinks, lay probably outside or at the edge of the fundamental niche and maintenance has to be ensured by continuous colonisation from the source populations in heathland or chalk grasslands. Other at first sight non-typical grey dune species have large populations, some even in the more distant AWD-dunes. Grey dunes are for these species certainly good-quality habitats and their absence in the isolated region has to result from their inability to bridge the matrix of non-suitable habitat. A reduced ballooning performance is hence to be expected in these species, as this is the most important mode for distant dispersal [Bonte *et al*. 2003c]. Ecological time [Pianka 1994] is hence an important process for the structuring of spider assemblages in coastal dunes along the North Sea. In spiders, similar patterns of differentiated species presence have been observed on inland dunes in the lowland of Germany [Merkens 2002].

Species occurring in the isolated regions should as a result possess a well-developed dispersal. Unfortunately, no ballooning data are available for most of these species. For other arthropods, carabid beetles [Desender *et al*. 1995; Turin 2000] and butterflies [Bink 1992], similar distribution patterns are observed and dispersal capacities can be directly measured [wing development in carabid beetles] or directly observed [migration propensity]. In these groups, xerothermic species from heathland and chalk grassland, absent in the Belgian coastal grey dunes, but present in the coastal dunes of the Netherlands and the Boulonnais have lower dispersal abilities, compared to species present in the Flemish coastal dunes [Bonte, unpub. data]. Butterflies absent in the Flemish coastal dunes had a significant lower rang of migration behaviour [Bink 1992], while carabid beetles, only present in the dune region of North Holland are significantly more brachypterous [Turin 2000; Desender *et al*. 1995]. Geological [historical] habitat isolation and ecological time is thus, at least partially, responsible for the observed species paucity of coastal grey dunes in Belgium and AWD.

Our data consequently indicate that differences in dune dynamics, latitude and connectivity to other xerotherm habitats influence the species composition of spiders in coastal grey dunes along the coast of the North Sea. The assemblage composition of spiders in grey dunes is as a result determined by sand dynamics and the linked habitat instability [Bonte *et al*. 2002a] and by ecological time.

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Appendix 1 - Abundance [number of individuals/#traps] of the non-eurytopic species from coastal grey dunes, with indication of their optimal habitat and abundance in the sampled coastal grey dunes, chalk grassland and heathland. Abundance legend: rare -r-: abundance<0.1; fairly common -fc-: abundance [0.1-0.5] ; common -c-: abundance > 0.5

Species	habitat	Chalk	BOUL	FCD	AWD	PWN	Heath
Acarthauchenius scurrilus [O.P.-Cambridge, 1872]	xerotherm		r	r		r	r
Aelurillus v-insignatus [Walckenaer, 1802]	chalk/heathland				fc	c	c
Agroeca cuprea Menge, 1873	xerotherm		fc	c	c	c	c
Agroeca lusatica [L. Koch, 1875]	heathland				fc	c	c
Agroeca proxima [O.P.-Cambridge, 1871]	xerotherm		c	c	fc	c	c
Alopecosa barbipes [Sundevall, 1833]	xerotherm	c	c	c	c	c	c
Alopecosa cuneata [Clerck, 1757]	xerotherm		c	c	c	c	c
Alopecosa fabrilis [Clerck, 1757]	xerotherm		c	c	c	c	
Araeoncus humilis [Blackwall, 1841]	chalk/heathland	fc			r		r
Arctosa perita [Latreille, 1799]	xerotherm		c	c	fc	fc	
Argenna subnigra [O.P. Cambridge, 1861]	xerotherm		c	c	c	c	fc
Atypus affinis Eichwald, 1830	chalk/heathland	fc	fc				
Aulonia albimana [Walckenaer, 1805]	chalk/heathland				fc	c	c
Centromerus incilium [L. Koch, 1881]	North				c	c	c
Ceratinopsis romana [O.P.-Cambridge, 1872]	coastal dunes		c	c	fc		
Cercidia prominens [Westring, 1851]	heathland					r	fc
Cheiracanthium erraticum [Walckenaer, 1802]	chalk/heathland		r			r	
Cheiracanthium virescens [Sundevall, 1833]	xerotherm		fc	c	fc	c	
Clubiona frisia Wunderlich and Schütt 1995	xerotherm		r	r	r	fc	
Crustulina guttata [Wider, 1834]	heathland					r	c
Diplocephalus graecus [O.P-Cambridge, 1872]	South			c			
Drassodes cupreus [Blackwall, 1834]	xerotherm	c	c	fc	fc	c	c
Drassodes lapidosus [Walckenaer, 1802]	xerotherm		fc	fc	fc	fc	
Drassodes pubescens [Thorell, 1856]	xerotherm	c	r	fc	r	r	
Dysdera erythrina [Walckenaer, 1802]	chalk	c	r				
Erigone promiscua [O.P.-Cambridge, 1872]	xerotherm	c	c	c	r		
Euophrus herbigrada [Simin, 1871]	chalk		r				
Euryopis flavomaculata [C.L. Koch, 1836]	chalk/heathland	fc	r	r	r	fc	fc
Evarcha falcata [Clerck, 1757]	chalk/heathland	fc	r				
Hahnia montana [Blackwall, 1841]	chalk/heathland	c	c			r	
Hahnia nava [Blackwall, 1841]	xerotherm	c	r	c	c	c	c
Haplodrassus dalmatensis [L. Koch, 1866]	xerotherm	r	c	c	fc	fc	
Haplodrassus signifer [C.L. Koch, 1839]	xerotherm		c	c	c	c	c
Haplodrassus umbratilis [L. Koch, 1866]	chalk/heathland		r			r	
Hypsosinga albovittata [Westring, 1851]	xerotherm	r	c	c	fc	c	
Hypsosinga pygmaea [Sundevall, 1832]	chalk	fc	r				
Lathys puta [O.-P. Cambridge, 1861]	chalk	c	c				
Lepthyphantes mengei Kulczynski, 1887	heathland				r	r	
Marpissa nivoyi [Lucas, 1846]	xerotherm					r	
Mastigusa aerietina [Thorell, 1872]	xerotherm			r			

Species	habitat	Chalk	BOUL	FCD	AWD	PWN	Heath
Mecopisthes peusi Wunderlich 1972	South	r	c				
Metopobactrus prominulus [O.P.-Cambridge, 1872]	xerotherm		r	fc		fc	c
Micaria dives [Lucas, 1846]	xerotherm			fc	r	fc	
Micrargus subaequalis [Westring, 1851]	chalk/heathland					r	
Ozyptila atomaria [Panzer, 1841]	xerotherm	c	fc	c	fc	c	c
Ozyptila nigrita [Thorell, 1875]	chalk/heathland	c	c		c	c	c
Ozyptila sanctuaria [O.-P. Cambridge, 1871]	South	fc	c			r	
Pardosa hortensis [Thorell, 1872]	South	r	r				
Pardosa monticola [Clerck, 1757]	xerotherm	c	c	c	c	c	fc
Pelecopsis nemoralis [Blackwall, 1841]	coastal dunes		c	c		r	r
Pellenes nigrociliatus [C.L. Koch, 1839]	South		r				
Peponocranium ludicrum [O.P.-Cambridge, 1861]	chalk/heathland	c	c		fc	c	c
Philodromus aureolus [Clerck, 1757]	South		r				
Philodromus fallax Sundevall, 1833	coastal dunes			r			
Phlegra fasciata [Hahn, 1826]	xerotherm	fc	c	c	fc	fc	
Scotina celans [Blackwall, 1841]	chalk	c	r				
Scotina gracilipes [Blackwall, 1859]	heathland	r				fc	fc
Scotina palliardi [L. Koch, 1881]	chalk/heathland	r	r			r	r
Sitticus distinguendus [Simon, 1868]	coastal dunes		fc				
Sitticus saltator [O.P.-Cambridge, 1868]	coastal dunes		c	c	fc		
Steatoda albomaculata [De Geer, 1778]	chalk		r				
Steatoda phalerata [Panzer, 1801]	chalk/heathland	c	fc		r	r	
Syedra gracilis [Menge, 1866]	South	c	r				
Textrix denticulata [Olivier, 1789]	heathland					r	
Thanatus arenarius Thorell, 1872	South		c				
Thanatus striatus C.L. Koch, 1845	xerotherm			r		r	
Trichopterna cito [O.P.-Cambridge, 1872]	xerotherm		c	c	c	c	
Typhochrestus digitatus [O.P.-Cambridge, 1872]	xerotherm		c	c	c	c	
Walckenaeria capito [Westring, 1861]	heathland					r	
Walckenaeria dysderoides [Wider, 1834]	heathland				r	fc	r
Walckenaeria furcillata [Menge, 1869]	chalk	r	r				
Walckenaeria stylifrons [O.P.-Cambridge, 1875]	South		fc	fc			
Xerolycosa miniata [C.L. Koch, 1834]	coastal dunes		fc	c			
Xysticus acerbus Thorell, 1872	chalk	c	c				
Xysticus erraticus [Blackwall, 1834]	xerotherm	c	c	fc	fc	c	r
Xysticus kempelini Thorell, 1872	South		fc				
Xysticus ninnii Thorell, 1872	South	fc	c	fc	c	c	
Xysticus sabulosus [Hahn, 1832]	coastal dunes		c	c			
Zelotes electus [C.L. Koch, 1839]	xerotherm		c	c	c	c	c
Zelotes latreilli [Simon, 1878]	chalk/heathland	c	c		fc	r	
Zelotes longipes [L. Koch, 1866]	xerotherm		c	c	c	c	
Zelotes pedestris [C.L. Koch, 1837]	chalk/heathland	c	fc			r	
Zelotes pusillus [C.L. Koch, 1833]	chalk/heathland	fc	r		c	c	c
Zelotes subterraneus [C.L. Koch, 1833]	heathland					r	

II.4 SPIDER ASSEMBLAGES FROM COASTAL DUNES: GENERAL DISCUSSION

FOTO: DRIES BONTE

Spider assemblages in the ecosystem of the Flemish coastal dunes were structured by variation in vegetation structure [succession], atmospheric and soil humidity and the presence of both natural and anthropogenic disturbance. Indicator species could be determined for almost all vegetation types.

Variation within the assemblages from different vegetation types clearly depends on the mean patch size of these habitats. Especially spatially separated [fragmented] habitats, with relative small patch areas are characterized by a large variation in species composition and defined as unstable assemblages. A more detailed study on the spider assemblages from grey dunes [moss dominated dunes and short grasslands] indicated that total species richness does not increase in function of the patch area. The total number of typical species is, however, larger in larger patches. These patterns potentially result from higher edge influences in small patches, the expected higher microhabitat variation in large patches or from higher extinction rates of species in small patches, not compensated by colonization events. Finally, patches are potentially too small to sustain sufficiently large populations.

Assemblages from large grey dune patches also show considerable local and regional variation within four distinct dune regions along the North Sea, with a different geological history and landscape structure. This variation can mainly be attributed to differences in local sand dynamics and the region. Species from dynamic dunes are mainly present in grey dunes from Belgium and France, while species from non-dunal xerotherm habitats [chalk grasslands and heathland] occur in both the Boulonnais and the North Holland dune region. These species are absent from the geologically young and isolated Flemish coastal dunes. Regional variation in spider assemblage composition hence results from local landscape characteristics [dynamics in the dune area], the latitude and the connectivity to non-dunal xerothermic habitats. This indicates the importance of landscape history and dispersal in structuring regional assemblages. Anecdotic, but interesting, is the occurrence of *Xysticus ninnii*, a species present in almost all sites from France and the Netherlands, but within the Flemish coastal dunes only present in the fossil dunes of Ghyvelde-Cabour, which are the oldest within the region [Janssen & Bonte 1998]. This species appears to be restricted in dispersal possibilities [see chapter III.2] and is probably incapable of reaching the younger complexes of the Flemish coastal dunes.

Although our analysis of the entire coastal dune assemblage is based on sampling campaigns, conducted during different years from the 1970's onwards, we believe that our indicator species are unambiguously identified with the IndicatorValue method [Dufrêne & Legendre 1997] by using presence/absence data. Year-to-year variation, however, may be responsible for the observed inter-habitat variation [Baert & Desender 1993; Desender 1996; Gajdos & Toft 2000]. As all habitat types, with exception of dune woodlands and the artificially created dune slack, were sampled during different years, we believe that different rates of variation cannot be attributed to these temporal aspects, but more to differences within the landscape structure, as demonstrated for the relation with the mean habitat patch size. The overall pattern of the assemblage structure is very alike those found for spider assemblages in coastal dune systems in other parts of Europe [Duffey 1968; Almquist 1973; Bell *et al.*, 1998] and for other invertebrate groups in the Flemish coastal dunes [Desender *et al.* 1992; Pollet & Grootaert 1996] and outside Belgium [*e.g.* Boomsma & Van Loon 1982].

Spider assemblage structure in coastal dunes follows hence the predictions of Pianka [1994], although we cannot discriminate between some potential mechanisms because they are related to each other. Especially patterns in habitat heterogeneity, productivity, microclimate and disturbance may be strongly interrelated. In coastal dunes, an increase of productivity is related to an increase in structural heterogeneity due to more complex vegetation structure, a loss of natural disturbance and an increasing microclimatological stability for species living within the vegetation. Only ecological time can be characterised as an independently functioning mechanism, especially at a larger geographic scale. *Ecological time*, i.e. the time needed by a species to colonise newly opened or remote areas of suitable habitat, proved to be of high importance in structuring spider assemblages in regions, with a different degree of connectivity and geological age. As species, for which suitable habitat is available, are absent from the most recent and isolated dune region, we can conclude that some species failed to colonise this region as from the time the habitat originated. At a shorter time span, the absence of species within suitable habitat, due to the failure to colonise small and isolated unoccupied patches can also been interpreted as a restriction of ecological time. We can hence explain the deficit of assemblage species richness by area and the isolation of the sites [Bruun 2000]. Our result are also in accordance with the theoretical framework, recently developed by Chase [2003], that history matters in designing multiple equilibria of the community assemblage when large regional species pools, low rates of connectivity and low degrees of disturbance occur. The dissimilarity between assemblages [?-diversity] increases as a result of these multiple equilibria among environmentally similar local communities. Only in the case of high dispersal rates between and within regions, ?-diversity will decrease, resulting in a single-equilibrium assemblage for which site history is of no importance [Chase 2003]. The similar assemblage structure between the two, only recently separated, dune regions in the Netherlands, confirms the prediction of the latter that more connected communities are more similar in species composition than less connected ones.

Our observed species-area relationship for stenotopic species in the spatially structured grey dune fragments along the Flemish coast can, however, indirectly depend on isolation and area, due to a loss of habitat heterogeneity and hence the absence of sufficient suitable microhabitats [Eriksson *et al.* 1995]. *Habitat heterogeneity* and *productivity* are narrowly linked in the coastal dune ecosystem and appeared to be the major determinant of the assemblage structure. This trend is widely accepted and documented for different taxa in coastal dune ecosystems [Duffey 1968; Van der Aart 1975; Almquist 1973; Koehler *et al.* 1995; Desender 1996; Pollet & Grootaert 1996, Bell *et al.* 1998; Mattoni *et al.* 2000]. In coastal dunes, highly productive habitats are often characterised by low depths of the ground water [in dune slacks] and aerial humidity will always be high, certainly if vegetation is well developed. This in contrast to exposed dry, low productive vegetation, where aerial humidity and temperature will show strong seasonal and daily fluctuations [Ampe & Langohr 1996]. Humidity effects, independent of effects of productivity, can hence be found in structural similar habitats with

different levels of humidity like managed grasslands [dry versus wet grasslands in dune slacks] and Marram dunes. Especially the separation of Marram dunes from the seaside and the inner dune front, stresses the importance of aerial humidity, as species, indicative for humid dune slacks [e.g. *Marpissa nivoyi, Tibellus maritimus, Clubiona subtilis*]. These species occur in relatively high numbers in Marram dunes near the sea and are almost absent in those near the inner dune front. This phenomenon has also been defined as "double ecological occurrence" [Duffey 1968].
Within grey dunes, habitat productivity *senso stricto* is of no importance in structuring local spider assemblages. This lack of any effect of productivity can be attributed to the narrow range of variation within the samples from grey dunes. Differences in productivity, reflected and measurable in the development of the soil A-horizon, have however significant effects on the presence of palatable springtails, which are the main prey for small spiders [Bonte *et al.* 2002e; Bonte & Mertens 2003]. These springtails are almost completely absent within the grey dune habitats during the summer and autumn but scarce on more productive, mesophytic grasslands during this period. The observed covarying phenology patterns of prey [springtail] and predator [stenotopic spiders], potentially masks an influence of productivity on the spider species compositions. Direct effects of habitat productivity [here prey abundance] are hence mostly pronounced during summer and autumn, and very similar during the winter and spring period. As this period corresponds with highest spider abundance and species richness, direct effects of productivity on higher trophic levels [spiders as predators compared to springtails as prey at a lower trophic level] will potentially be concealed.

Effects of *disturbance* have only rarely been documented as a direct assemblage-structuring parameter [Mattoni *et al.* 2000], although many studies focused on management effects [e.g. Gibson *et al.* 1992; Bonte *et al.* 1999; Bonte *et al.* 2000b; Dennis *et al.* 2001; Cattin *et al* . 2003]. Both aeolian and management disturbance were the third important factor influencing spider assemblages in the Flemish coastal dunes. Although the effects of nature management cannot *a priori* be disentangled from parameters related to vegetation structure, productivity and microclimate, differences in species composition between artificial restored dune slacks and natural formed ones, document clearly the influence of even nonrecurring disturbance effects. In these not the absence of expected species [which is more an ecological time effect] but the dominance of eurytopic species highlights the influence of disturbance on the spider assemblage. The ordinations of habitats, characterised by aeolian dynamics, in the same direction as the management-disturbed sites, indicate similar influences on the spider assemblage. As predicted by Pianka [1994], species occurring in these habitats are generalists or strong specialists. Generalists have a broad niche spectrum and are often referred to as ruderal species [maximal IndVal levels at low levels in the TWINSPAN hierarchy]. In contrast, highly specialised species have narrow niche breadths [species as *Philodromus fallax*, only occurring in these sandy dynamic habitats]. The latter are completely absent in case of management disturbance. Within grey dune habitats across the four investigated regions, the magnitude of aeolian disturbance is even the major determinant of species variation. The presence of species, related to sand dynamics is hence responsible for the variation between and within spider assemblages in the four regions. We believe that the absence of typical coastal dune species in grey dunes of the Netherlands, with nowadays locally similar magnitudes of dynamics, originates from the total dune landscape structure, influenced by historical stringent large-scale fixations of dynamic sandy dunes. Again, this similar history decreases the β-diversity between the investigated Dutch dune regions. The prediction that more disturbed regions [Flemish coastal dunes, Boulonnais] are more similar in community structure than less disturbed regions [Chase 2003] does not hold in our study. Probably, historical and climatic factors overrule the effect of disturbance in shaping similar assemblages or disturbance is not high enough to induce a decrease of the local [$=\alpha$] diversity, resulting in a low β-diversity [Connel 1978].

In addition to Pianka's [1994] potential mechanisms responsible for the structure of species assemblages, both *edge effects* [at the local and regional scale] and *latitude* [at the regional scale] determine the distribution of spider species in coastal dune habitats. As epigeic[8] spiders are mobile, assemblages in small fragments are strongly influenced by the species composition of the *neighbouring habitats*. This can be deduced from the negative relation between the assemblage stability and the mean area of the respective habitat and from the fact that the species-area relationship for all species, in contrast to the specialised ones, does not show a significant trend in function of the patch size. Analogue results were observed in spider assemblages from German inland dunes [Merkens 2002]. Species intruding apparently hostile habitats, can in this way survive outside their fundamental niche, although local mortality can exceed recruitment in case of a source-sink dynamics [Pulliam 2000]. If our observed edge effects would implicate the presence of vital populations, and not sporadic excursions outside the native habitat, this would address the possibility that these species can extend their fundamental niche into a broader realised niche. These sink populations can as a result only survive if dispersal assures continuous colonisation out of the source-matrix.

Although not explicitly investigated, our results indicate that climatic factors influence the distribution of species. Annual temperatures show a small but significant differentiation in function of the latitude and increase from North-Holland [De Kooy: mean temp. of 9.4°C][9], South Holland [Vlissingen: mean temp. of 10°C][9], Flanders [Koksijde: 10°C][10] to the Boulonnais region [Boulogne-sur-Mer: 10.3°C][11]. Regional microclimatic differentiation is believed to correspond with this macroclimatic differentiation, because of the similar sampled habitats. In contrast to precipitation and wind velocity, which do not show consistent differences between the sampled regions[9-11], only temperature is assumed to determine species distribution because of its influence on species' life histories [Pianka 1994]. Other climatic factors probably influence species' activities and are the reason why data were analysed by presence/absence records and not on absolute or relative activities [number of trapped individuals]. Because of the small latitudinal range and the overruling influence of local landscape features [see higher], our data do not show a decreasing total species rich-

[8] *Species living above the soil surface*

[9] *www.klimadiagramme.de*

[10] *Ampe & Langohr [1996]*

[11] *Thumerelle [1993]*

ness with increasing latitude [Pianka 1994]. Interesting is the decreasing number of species, living at the Northern limit of their range within the small latitudinal gradient: stenotopic species, with a more Southern distribution are better represented in in the Boulonnais region than in Flanders [e.g. *Mecopisthes peusi, Pellenes nigrociliatus, Thanatus arenarius, Xysticus kempelini*] and are almost absent from the Netherlands coastal dunes. An annual temperature difference of [less than] 1°C is as a result reflected in the spider species composition. If some of these species have a well developed dispersal capacity or if they are able to change their dispersal capacity [Thomas *et al*. 2001], range expansion can be expected in function of climate change, as already documented for the Mediterranean species *Diplocephalus graecus* [Bonte *et al*. 2002b].

In conclusion, we demonstrated that spider assemblages within the entire ecosystem of the Flemish coastal dunes and from grey dunes in four different regions are in general influenced by ecological time, disturbance and mechanisms related to the productivity of the habitat [vegetation succession, humidity, habitat heterogeneity]. As epigeic spiders are mobile, edge effects are assumed to determine additional variation within and between assemblages from the same habitat. Because we were able to identify indicator species for almost all relevant habitat types, different assemblages can be recognised in function of the vegetation structure. As dispersal is crucial in structuring species distribution, population structure and species ranges at large geographical scales or within local patchily distributed populations [Loreau & Mouquet 1999; Thomas & Kunin 1999], I present results on its evolutionary and ecological importance in part III of this thesis.

III.1 EVOLUTIONARY AND ECOLOGICAL ASPECTS OF DISPERSAL, WITH EMPHASIS ON SPIDER DISPERSAL BEHAVIOUR

FOTO: WWW.ARACHNOLOGY.ORG

Movement, migration and dispersal

Animal and plant movements are one of the most studied, yet least understood concepts in ecology and evolutionary biology. The motivations, causes and consequences are affected by ecological and behavioural parameters like growth forms, seasonality, habitat and social systems [Clobert *et al.* 2001]. This movement has consequences for the individual, the population and the species distribution. As a result of its effect on the inclusive fitness[12], selective forces affect the distribution, abundance and dispersion of individuals.

As shown by Dingle [1996] in his book "*Migration, the biology of life on the move*", movements can take many forms, from foraging to migration and accidental displacements. The term *dispersal* has often been confused with *migration*. Migration is used to define *cyclic* individual movements across habitats, *beyond* the home range, whereas dispersal is used within the context of presumptively *one-way movements* and usually applied to individuals moving to breeding locations *away* from the place they were born, often within the individual home range. Dispersal occurs rarely throughout the entire life-cycle of organisms, is restricted to specific life stages, and often related to morphological characteristics and physical constraints determined by the environment [Dingle 1996].

The evolution of dispersal

Dispersal is a life-history trait that has profound evolutionary consequences as it potentially determines the level of gene flow between populations and affects processes such as local adaptation[13], speciation and the evolution of life history traits. In the last decades, several mechanisms have been identified that influence the evolution of dispersal strategies. These theoretical studies are mainly based on mathematical models for game theory and seek to delineate *Evolutionary Stable Strategies [*Dieckmann *et al.* 1999]. In contrast to the extensive literature on the possible mechanisms that affect the evolution of dispersal, a serious gap exists between theory and data [Dieckmann *et al.* 1999].

Mathematical models, using Evolutionary Stable Strategies [ESS], predict that the evolution of dispersal is *selected against* by

- ***Intrinsic costs*** [Hamilton & May 1977]: if dispersal is costly, because of mortality during travelling or investments into dispersal morphology, optimal dispersal rates will decrease.
- ***Stable environmental heterogeneity and spatial variability*** [Holt 1985; Doebeli & Ruxton 1997; Parvinen 1999; Mathias *et al.* 2001] and ***predictability of habitat quality*** [Southwood 1962; Van Valen 1971; McPeek & Holt 1992]: in stable, spatially heterogeneous habitats, risks of local extinctions are low and dispersal should, because of the affiliated costs [low chances in reaching suitable habitat, which are patchily distributed], not evolve towards high dispersal rates. Temporal predictability of the habitat quality selects against dispersal because organisms experience certainty of resources in the local habitat and do not need to invest in displacements. In case habitats fluctuate both spatially and temporally, optimal dispersal rates depend on how both are correlated.

In contrast, increased levels of dispersal, are selected by:

- ***Kin competition*** [Hamilton & May 1977; Perrin & Lehman 2001; Lehman & Perrin 2002]: competition among kin selects for dispersal as it reduces competition between close relatives, even in the absence of other dispersal-promoting factors, such as unstable habitats.
- ***Inbreeding depression*** [Chesser & Ryman 1986; Perrin & Mazalov 1999; Perrin & Mazalov 2000]: costs of inbreeding can also select for dispersal and are independent of competition between kin. The avoidance of inbreeding additionally selects for a sex-biased dispersal [Pusey 1987; Motro 1991], in which the most common sex is the disperser. In polygynous mating systems, a male-biased dispersal is selected to reduce inbreeding within the natal population and to reduce male-competition [e.g. Greenwood 1980, Dobson 1982; Greeff 2002].

12 The expected contribution of an allele, genotype or phenotype to future generations, relative to the contribution made by others in its present population [Begon et al. 1996; Stearns 1992]

13 Characteristics of organisms evolved as a consequence of natural selection in its evolutionary past and which results in a close match with features of the environment and/or constrain the organism to live in a narrow range of environments [Begon et al. 1996]

Empirical evidence of these potential causes of dispersal is however scarce, certainly because a comparison of interspecific differences in dispersal traits of even closely related species needs the integration of phylogenetical independent contrast [PIC's], in order to correct for potential covarying evolutionary adapted traits [Stearns 1992]. These contrasts become slowly available, as a result of the increased use of genetic markers in phylogenetical cladistics. Evidence for the existence of these potential mechanisms in arthropods is summarised hereafter.

Roff [1977] documented the energetic costs of active dispersal in Diptera, which was reflected in a reduced egg production. As costs decreased with increasing size, the probability of dispersal was size dependent, and small flies dispersed at lower probabilities. According to Berwaerts *et al.* [2002], the acceleration capacity of the butterfly *Pararge aegeria* was also related to morphological characteristics such as body mass and wing loading, indicating that costs of dispersal are higher in smaller butterflies. According to Thomas *et al.* [1998], these traits may have a heritable component and have therefore the potential to respond rapidly to selection acting on flight morphology. In the bivoltine butterfly, *Araschnia levana*, the summer generation is characterised by a larger relative wing size and lower wing loading. Individuals from this generation have a higher mobility [Fric & Konvicka 2002], although other mechanisms leading to this variation of mobility, like temporal variation in habitat quality, were not studied. Similarly, the effect of a lower wing size, relative to the body size led to increased energetic costs in a Pierid butterfly [Kingsolver 1999]. Nevertheless, initial dispersal rates or survival did not differ between manipulated butterflies and the control group [Kingsolver 1999], indicating that apparent selection for dispersal in function of intrinsic costs should not *a proiri* be related to these. Other selection mechanisms may hence be more important in shaping dispersal patterns. The cost of dispersing also increases as the distance between patches increases and connectivity decreases. Hence, from a certain degree of isolation onwards, selection against dispersal-related traits may be expected [Dempster *et al.* 1976; Dempster 1991; Leimar & Norberg 1997; Norberg & Leimar 2002].

Selection pressures, related to the habitat stability and predictability is best documented in arthropods. The concept of a decreased mobility of species living in predictable and stable habitats was first proposed by Southwood [1962]. Extensive empirical evidence is available for butterflies [as can be deduced from data in Bink 1997; Maes & Van Dyck 1999], carabid beetles [Desender 1987; Desender 1989b; Den Boer 1999], water bugs [Kaitala 1988] and for spiders of the genus *Pardosa* [Richter 1970; Greenstone 1982]. Richter [1970] however, could not substantiate this hypothesis because of his confusing definition of the stability of the habitat. In island plant populations, a reduced selection for wind dispersal has been observed for generalist anemochorous weeds, in comparison to mainland populations, and potentially enhances a strong local adaptation to the environment [Carlquist 1966; Cody & Overton 1996], although the latter has not been investigated or documented.

The avoidance of competition among kin can also select for dispersal, although mainly documented in marine invertebrates [Kasuya 2000] and birds [*e.g.* Yates *et al.* 2000; Cale 2003]. Many studies, however, did not find any selection due to kin competition [Wheelwright & Mauck 1998; Bodasing *et al.* 2002; Krackow 2003]. In social species, dispersal can be selected against due to philopatric benefits [like helping behaviour], as documented for vertebrates [*e.g.* Lessels *et al.* 1994] and invertebrates [Johannesen & Lubin 2001; Powers & Aviles 2003]

Empirical evidence of selection for inbreeding avoidance is even scarcer, and studies on sex-biased dispersal can often not distinguish between inbreeding avoidance or the effect of male competition. Even if general patterns are consistent with predictions of the inbreeding-avoidance hypothesis, this hypothesis should not predict the observed sex-biased [male-biased] dispersal patterns, and evidence is often given against [Caley 1987; Duarte *et al.* 2003]. Direct studies on increased dispersal rates in case of inbreeding often fail to prove evidence [Negro *et al.* 1997], due to the interference of trade-offs with benefits of restricting natal dispersal, as the availability of suitable habitat [Daniels & Walters 2000]. The relationship between inbreeding avoidance and dispersal has until now only been documented for birds [Greenwood *et al.* 1978; Vantienderen & Vannoordwijk

1988; Byholm *et al.* 2003] and mammals [Bollinger *et al.* 1993].

Evidence supporting the hypothesis of Kisdi [2002] that risk spreading in stochastic environments and adaptation to permanent properties of local habitats interplay in the simultaneous evolution of dispersal and habitat specialisation is not available [with exception of Bonte *et al.* 2003d, see III.2]. Because of the apparent large cost of passive aerial dispersal in fragmented landscapes and islands, we expect positive selection if the individual benefits from the dispersal. Natural selection should reduce well-developed aerial dispersal behaviour, if the risk of landing in an unsuitable habitat is high or if the species is strictly specialised to the habitat. Selection for dispersal in generalists should as a result favour risk spreading because of a suboptimal adaptation to the local habitat, while dispersal is selected against in specialists by a strong adaptation to local environmental conditions.

Obviously, these theoretical adaptive mechanisms interact in shaping dispersal patterns in populations. Variation in dispersal ability will be additionally determined by postnatal environmental effects, which sum and interact with the adaptive component [Ims & Hjerman 2001]. These multiple selective forces underlying the dispersal pattern of populations, at different spatial scales, are responsible for observations of apparently unusual high or low dispersal rates in function of one of these selective mechanisms [Ferriere *et al.*, 2000]. Especially high dispersal rates in function of the habitat stability may have been shaped by other selective pressures or by specific environmental triggers. In spiders, for example, the observed dispersal frequencies in the obligate burrowing and cursorial resident *Geolycosa*-species from stable habitats are unexpectedly high [Miller 1984]. Although habitat stability was derived from climatological data and not from other potential environmental factors like the stability of the habitat structure [vegetation succession] or natural sand dynamics, the observed high frequencies may result from selection against inbreeding as wind dispersal is in these species the only relevant dispersal mode, enabling offspring to avoid kin for mating or from selection against kin competition if resources are limited in the neighbourhood of the nest.

The genetic basis of dispersal

The increasing evidence on variation in dispersal shows that traits, related to dispersal, are not randomly expressed between and within populations, but evolutionary determined. As additive variation[14], often expressed as heritability[15] h^2 [ratio of the additive variation on the total phenotypic variation[16] V_A/V_P], is the key-source for evolution, quantitative genetic analyses[17] were applied to determine the magnitude of the adaptive value [Lynch & Walsh 1998; Mazer & Damuth 2001; Roff & Fairbairn 2001]. The dispersal capacity can be expressed in morphological, behavioural and physiological traits, which are [often relatively] easy to measure under field and laboratory conditions. These sources of phenotypic variation were used for heritability estimates by sib-analysis and artificial selection [Dingle 1996].

Individuals within a population are often divided in two groups: dispersers and non-dispersers, each with its typical set of life history, morphological, behavioural and physiological characteristics. This dichotomization, however, is often misleading as it implies a very particular and unlikely Mendelian genetic architecture underlying these traits [Roff & Fairbarn 2001], although the latter exist in the Mediterranean bug *Horvathiolus gibbicollis* [Solbreck 1986]. Genetic variation in traits related to dispersal, appears often to be under polygenic control [Dingle 1996], as extensively demonstrated and reviewed by Roff & Fairbairn [2001], for wing dimorphism of insects, the body morph in salmon, behavioural traits as flight duration, anemotaxis, settling behaviour in insects, migratory behaviour in birds and physiological characteristics as metabolic enzyme activity and flight muscle histolysis. Even less obvious dispersal characteristics, as behaviour-at-boundaries, can rely on heritable variation [Merckx *et al.* 2003], although the latter did not

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[14] The variance among individuals in breeding values [Stearns 1992]

[15] Proportion of the total phenotypic variance among individuals in a population that is accounted for by additive genetic variance [Stearns 1992]

[16] Variation in the expression of genotypes in interaction with the environment during the course of the growth and development of the organism [Stearns 1992]

[17] The genetics of a trait that varies continuously and that are determined by large number of genes each with relatively small effects. It is a statistical method of inferring genetic influences from phenotypic variation. [Stearns 1992]

control for genetic correlations with other adaptive traits or maternal effects. The estimated heritabilities are, with exception of some behavioural traits, larger than 0.30, indicating that these traits may rapidly respond to selection. This potential fast microevolution[18] has been observed in artificial selection experiments on beetles *Tribolium* [Dingle 1984], bugs *Oncopelthus* [Palmer & Dingle 1986; Palmer & Dingle 1989], crickets *Gryllus* [Roff 1990] and the warbler *Sylvia atricapilla* [Berthold 1988]. According to Roff [1986b], the polygenetic[19] control of the expression of traits, narrowly linked to dispersal, can be explained by the fact that [i] many factors contribute to the dispersal behaviour and are associated within physiological and life-history traits and [ii] due to the presence of many response patterns on the selective pressure in polygenetic systems.

Additionally, many traits that contribute directly to the individual fitness [fecundity, body size, development time] often correlate with dispersal-linked traits, although not always in the same direction [Roff & Fairbairn 2001]. These patterns of genetic correlation[20] indicate that dispersal *in se* can covary and trade-off against morphological or life-history characteristics and that selection on morphological or life history traits indirectly can select for or against dispersal, or *vice versa*. Genetic correlations come about through either by linkage or pleiotropy[21], and pleiotropy seems more likely for migration or dispersal syndromes because genetic linkages tend to be broken up by recombination events over time [Dingle & Holyoak 2001]. Variation between individuals from the same species or from the same population can point towards the presence of mixed emigration strategies within the population [Weyman *et al.* 2002]. Particularly, when the benefits associated with a particular behaviour also depend on the behaviour of others, the ESS may be to have a mixture of behaviours [Maynard-Smith 1974, Maynard-Smith 1976]. According to Parker & Stuart [1976], mixed dispersal

[18] *Minor evolutionary event usually viewed over a short period of time [few generations] within a population [Lincoln 1982]*

[19] *A trait influenced by the expression of many genes*

[20] *The portion of a phenotypic correlation between two traits in a population that can be attributed to additive genetic effects [Stearns 1992]*

[21] *One gene affects two or more traits [Stearns 1992]*

strategies, which often appear to be randomly expressed, within a population could result from a genetically monomorphic population, in which individuals are evolutionary determined to select different emigration thresholds from the same probability distribution, based on their individual perception of the resource quantity and quality; or it could result from genetic polymorphism with respect to the threshold values of resources that trigger emigration, whereby each individual always has the same threshold.

Proximate mechanisms of dispersal: the influence of the environment

In addition to the above described genetic adaptive mechanisms underlying the dispersal propensity or dispersal rate of organisms [*innate factors*], environmental mechanisms may influence dispersal patterns [*proximate factors*]. Both processes originate similarities in dispersal behaviour among siblings [Massot & Clobert 2000].

The pathway between the environment and the final dispersal event can be a direct behavioural response of the organism towards the environment [*e.g.* photoperiod, good weather conditions, scarcity of prey, crowding conditions…] or indirectly mediated by the phenotype that was directly influenced by the environment [a changed *internal* condition]. Examples of the latter are an increasing dispersal resulting from a decrease in growth rate or a change in hormonal [or energetic] state, due to a bad habitat quality. The environment hence influences the condition of the organism, which will be the direct trigger to disperse and not the environment *per se* [Ims & Hjerman 2001]. According to Massot & Clobert [2000] condition-dependent dispersal, can be prenatal and postnatal. Postnatal condition-dependent dispersal mechanisms include the direct effects of the environment on the organism, after it was born, so changes in the condition during its life. Prenatal conditions, on the other hand, are effects of the environment on the organism's condition during the embryonic development and include maternal effects[22]. If maternal effect are linked with the internal conditions, a time lag will be present between the environmental cue and the expres-

[22] *All phenotypic effects in the progeny that can be associated with the mother but not attributed to her breeding value [Stearns 1992]*

sion of the dispersal trait. These maternal effects can be involved when phenotypic specialisation for dispersal takes place at an early ontogenetic stage [during early juvenile development], and when the offspring are not capable of perceiving cues from the external environment. In this sense, a maternal link in the pathway of condition-dependent dispersal conveys information about the environment not yet accessible to the offspring [Ims & Hjermann 2001]. These responses may help the offspring to settle successfully in their natal environment or to increase their likelihood to disperse [De Fraipont *et al.* 2000]. Although maternal effects are often interpreted as a non-genetic form of heredity [Sorci *et al.* 1994], they can be evolutionary significant if genotype and environment strongly correlate and if maternal effects increase offspring fitness or when maternal effects differ between maternal genotypes [Mousseau & Fox 1998; Mazer & Damuth 2001].

These three different pathways, in which the environment influences the dispersal pattern of organisms is visualised in Fig. III.1-1 [after Ims & Hjermann 2001].

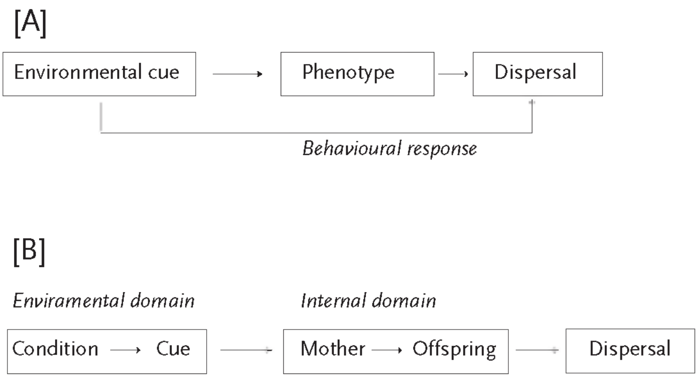

Fig. III.1-1. Alternative causal pathways between an environmental cue and the consequent dispersal response. [A] Direct pathways following an immediate behavioural response and indirect pathway mediated through a change of the phenotype. [B] Extended, indirect pathways, due to several links in the environment and internal domains [after Ims & Hjermann 2001].

Typical examples of direct reactions towards characteristics of the habitat are responses to *resource deprivation* [*food availability*: Ward 1986; Weyman & Jepson 1994; Kreiter & Wise 2001; Matter & Roland 2002; *host abundance*: Matter & Roland, 2002; Hanski 1999a; Hanski et al. 2002], *the season and photoperiod* [Croach & Lubin 2001; Ide 2002], *climate* [Croach *et al*. 1998; Isaacs & Byrne 1998], *substrate mimicry* [Morse 1993; Altmoos 2001], soft patch *boundaries* and a small patch *size* [Zollner & Lima 1997; Boudjemani *et al*. 1999; Ries & Debinski 2001; Berggren *et al*. 2002; Merckx *et al*. 2003] and the reaction towards *tidal regimes* [Morse, 1997; Morse 2002]. The *nature* of the population can also be seen as a direct environmental cue in for instance the case of low population densities, resulting in unusually high dispersal rates and an Allee-effect[23] [Kuussaari *et al*. 1998; Matter & Roland, 2002; Ménendez *et al*., 2002].
A classical example of the indirect effect of the environment on dispersal, due to changes in the phenotype is found in the bug *Oncopeltus fasciatus* [Dingle 1986]. Here, the temperature during the juvenile development changes the species physiology and significantly influences its wing morphology. Desender [1989a] performed similar experiments on the wing development of the carabid beetle *Pogonus chalceus*, but found no effects of the environment.

Although no direct evidence is available, homing behaviour that restricts dispersal [Zeil 1998; Conradt *et al*. 2001], can also be interpreted as indirect effects through a change of the phenotype [experience]. This cryptic phenotypic change influences as a result dispersal behaviour. In conclusion, indirect effects of the environment, through a change of the phenotype, occur in nature but are probably not universal and in some cases very subtle and hard to detect.

The expression of maternal characteristics has been shown to occur through alterations of offspring size [Massot & Clobert 2000], clutch size [Diss *et al*. 1996], sex ratio [Ims 1990; Massot & Clobert 2000], maternal odour [Léna *et al*. 2000], female stress resulting in higher corticosterone

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[23] *An Allee effect occurs where individuals in a population have a disproportionately low rate of recruitment when their own density is low [Begon et al. 1996]*

contents [De Fraipont *et al.* 2000] and maternal parasite load [Sorci *et al.* 1994]. Females can also influence offspring dispersal by their selection of the natal habitat in function of the social environment, local population structure [Ims 1990; Hanski *et al.* 1991] and habitat quality [Morse 1993; Diss *et al.* 1996].

The environmental domain can additionally determine the expression of dispersal in a genetical way, but without any adaptive significance for dispersal, as genetic correlations with traits evolved as adaptations to the habitat or landscape type [Roff 1997; Mazer & Damuth 2001]. Due to the loss of pleiotropic or linkage interactions, genes coding for dispersal may become afunctional [Roff 1997].

Population-dynamic and population-genetic consequences of dispersal

The most widely considered effect of dispersal at the scale of the local population is regulation of the population size through density dependent emi- and immigration, although dispersal may affect population dynamics in other ways. In small populations, the lack of immigration or increased emigrations [Courchamp *et al.* 1999] may increase the risk of extinction. Conversely, immigration may rescue small populations from extinction by mediating the population size [ecological rescue effect] or maintaining genetic diversity [genetic rescue effect]. At the metapopulation level, dispersal is essential for the persistence of the total population in a fragmented landscape, due to sequential colonisation-extinction events. Dispersal can be viewed as a form of risk spreading, which enhances growth rate and hence the persistence of the metapopulation, consisting of local population with independent dynamics. In this way, dispersal may be the means by which prey and predator or species with different competitive abilities can co-exist. It additionally enhances the persistence of population in sink habitats [with a negative growth rate] due to a continuous colonisation out of source populations, often with high emigration rates due to density-dependent dispersal patterns.

Especially in the last decade, population dynamical consequences, both at the level of the population and the metapopulation have received much attention [e.g. Hanski 1994; Doebeli & Ruxton 1997; Hanski 1999a; Hovestadt, 2000; Poethke *et al.* 2003]. Because of difficulties in studying these patterns in nature, theoretical papers are dominant and lack in many cases empirical evidence.

In spatially separated populations, dispersal promotes gene flow. As these structured populations experience spatially-dependent selection pressures, gene flow will be evolutionary important in structuring these adaptive processes. It is however not obvious that gene flow of advantageous alleles has to alter long-term patterns of selection, because the chance that they will fix is largely independent of the population structure, provided that they nowhere decrease fitness [Maruyama 1970, *In*: Barton 2001]. The theoretical mechanisms of how dispersal or no dispersal [isolation] affects evolution are well developed, but empirical evidence on the relative importance of these mechanisms is, again, very scarce.

Divergence between separated population through random drift was proposed by Wright [1931, 1943] for islands, in which the number of migrants m relates to the genetic differentiation F_{ST} following the equation $F_{ST}=1/[1+4Nm]$, in which N is the local population size. According to Barton & Whitlock [1997], drift reduces the genetic variance within populations, while the load due to additive deleterious mutations increases. Because random drift has only marginal influences on fitness, it is hence unlikely to have a significant effect under severe selective pressures and can, consequently, not influence evolution through the spatial differentiation. Inversely, the indirect measure of gene flow by the described equation is not correct because of the biologically unrealistic underlying assumptions of no selection, no mutation, equal numbers of emi- and immigrants in the subpopulations and a completely random dispersal [Whitlock & McCauley 1998].

Whether populations can adapt to local condition in spatially separated systems, depends essentially on the rate of gene flow and adaptive selection [Barton 2001]. In general, an allele with a selective advantage can be established into a population, despite gene flow, provided that the rate of immigration of individuals carrying an alternative is lower than the rate of selection [Haldane 1931, *In*: Barton 2001]. Empirical evidence of this overruling importance of selection in spatially separated populations, even with a substantial amount of gene flow, was given by Mallet [1993] for different mimicry rings in butterflies, in populations only 10 km or less separated and by MacNair [1987], in heavy metal-tolerance in a grass on mines, only a few meter wide. Hendrickx *et al.* [2003] obtained similar results for adaptive reproductive variation in function of heavy metal tolerance in saltmarshes situated along the Scheldt river. This selection may favour habitat specialisation within local populations and a selection against dispersal under circumstances where gene flow acts against the specific local adaptive pressure selection. Obviously, if gene flow strongly acts against a necessary local adaptation, the loss of dispersal will increase the speed of local adaptation.

As mentioned above, dispersal has a strong effect on metapopulation dynamics and promotes colonisation of empty but suitable patches. If empty patches are colonised by a limited number of alleles, they will often be maladapted and growth rate of the population will slow down [Endler 1979]. Since new beneficial mutations or the input of well-adapted genes will as a result be responsible for a stronger and faster adaptation, newly founded populations, will faster adapt to changing local environmental conditions. Of course, if selective pressures are similar in all the local patches, divergence due to adaptive selection will not occur. Asymmetrical dispersal rates in a source-sink structure also have important consequences for adaptive evolution, as most of the individuals from the sink habitat trace their ancestry to immigrants from the source habitat [Kawecki & Holt 2002]. This asymmetrical gene flow makes adaptive selection in the sink unlikely [Kawecki 1995; Holt 1996a,b]. Sink habitats will thus persist in a state of permanent maladaptation as confirmed by numerous empirical studies [Dhondt *et al.* 1990; Blondel *et al.* 1992; Stanton & Galen 1997].

Dispersal in spiders

Spider can move in two ways: or by walking or running on the soil or in the vegetation, hereafter referred to as *cursorial* dispersal or via passive transport in air currents, so called *ballooning* if silk threads are used.

Cursorial dispersal

In wolf spiders and related families, cursorial dispersal reflects the most important mode of movement and dispersal [Bonte & Maelfait 2001; Kreiter & Wise 2001; Henschel 2002; Morse 2002]. It is linked to the overall pattern of high cursorial activity in this group of arthropods, mainly related to mate searching behaviour in males and to foraging and seeking of suitable micro-habitats for the deposition of egg-sacs in gravid females [Maelfait & Baert 1975]. Cursorial activity is generally assumed to be higher in males than in females, and this pattern is believed to explain the widespread male bias in pitfall records outside optimal habitat [Bonte & Maelfait 2001]. Costs of cursorial dispersal in spiders are on average low although mortality can be substantially high in population with high dispersal rates [Morse 1997]. In absence of mechanisms of patch recognition and homeward orientation, high levels of cursorial mobility may increase chances of diffuse patch emigration, especially when habitat boundaries are smooth [as in butterflies: Kuussaari *et al.* 1998]. At present there is a critical lack of empirical study on mechanisms of cursorial dispersal and orientation in invertebrates, and particularly on the link with population characteristics at the landscape level.

Aerial dispersal

Ballooning behaviour is, probably because of its aberrant character, extensively documented[24], although little is known of its ecological and evolutionary importance [Weyman *et al.* 2002]. The phenomenon was first described in 1678 by Martin Lister[25] [Salmon & Horner 1977]. According to Weyman *et al.* [1995], this mode of aerial dispersal can be described as a passive flight, generated by an upward drag on a silk thread, which induces a lift into air currents. In the case no upward currents are available, the thread can be released until it reaches an object, after which the spider detaches and climbs onto the object. This similar dispersal mechanism is

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[24] Excellently reviewed by Jeroen Vanden Borre [2002] in his graduate thesis 'Onderzoek naar het aeronautisch en kannibalistisch gedrag bij juveniele duinwolfspinnen [Pardosa monticola [Clerk, 1757] [Araneae, Lycosidae]] – Ghent University, 124 pp + appendices.

[25] A digital copy of this article can be downloaded from the website http://allserv.Ugent.be/~dbonte/research.htm

referred to as *bridging* [Henschel *et al.* 1995], *ridging* [Samu *et al.* 1999a] or *rappelling* [Greenstone *et al.* 1985a]. The behavioural mechanisms of the latter are assumed to be similar to the ballooning behaviour [Jones 1996a] although this has not been verified [Eberhard 1987]. Possibly both dispersal modes evolved in different ways, but resulted in a similar mechanism [Duffey 1998].

Ballooning is known from many arthropod groups, and defined as quasi-passive aeronauts by Suter [1999] because its presence in wingless arthropods [*passive* flight], but with behavioural adaptations. Besides in spiders, ballooning dispersal is known in caterpillars [Diss *et al.* 1996] and mites [Li & Margolies 1993]. Similar passive dispersal also occurs under the sea-surface, by bivalves, which drift in sea-currents by using byssus threads [Hiddink 2002].

Ballooning dispersal is known from many families of spiders [*e.g.* Salmon & Horner 1977; Dean & Sterling 1985; Bonte *et al.* 1998], including mygalomorpha [Coyle 1983; Coyle 1985]. Ballooning dispersal has been documented mostly from temperate regions [e.g. Richter 1970; Weyman *et al.* 1995; Duffey 1997; Duffey 1998; Thomas & Jepson 1999], but also from arctic [Coulson *et al.* 2003], subtropical arid or Mediterranean [Dean & Sterling 1985; Greenstone *et al.* 1987] and tropical regions [Robinson 1982, *In:* Decae 1987].

Behavioural mechanisms of aerial dispersal

Ballooning dispersal occurs through several possible behavioural adaptations, which can be divided into the ballooning behaviour *per se*, so during transport in air currents and the behaviour in preparation of the aerial dispersal [*pre-ballooning* behaviour]. The behaviour of the aerial dispersal [ballooning *per se*] is a largely unstudied field. In general, it is assumed that spiders cannot control their aerial transport, but Humphrey [1987] and Suter [1992] found indications of a certain, although probably marginal, “flight” control. Theoretically, spiders can control current drag [frictional] forces by changing the length of the thread [prolonging the thread will enable the spider to disperse larger distances] or changing the position of the body [Suter

1999]. The hypothesis of a changing thread length has only been theoretically approached [Humphrey 1987], but the change of the position and exposure of the body has been empirically observed and tested by Suter [1992]. The latter found that variation in dropping speed not solely could be explained by the variation in thread length, but that spiders, spreading their legs ["spread eagle posture", Suter 1999], experienced larger frictional forces resulting in a lower dropping speed. In this case, spiders facing unsuitable habitat may be able to slow down their landing in the chance of reaching a suitable environment. According to Weyman [1993], however, this hypothesis presumes an excellent visual perception of the environment [and a knowledge of whether it is "good" or "bad"] and is hence highly improbable, certainly for species with a bad vision [web-building spiders]. These behavioural mechanisms remain however speculative and certainly need further investigation, not at least because they are potentially influenced by different selective pressures.

In contrast, variation in the pre-ballooning behaviour is better documented [probably because it is more easily studied]. Best known is ***tiptoe*** behaviour [Fig. III.1-2A], firstly described by Bristowe in 1939 [Duffey 1998]: a spider stretches its legs and raises the abdomen, before the silk thread is produced from the spinnerets. Only when the thread is long enough to experience drag of air currents, the spider detaches into the air [Vugts & Van Wingerden 1976; Humphrey 1987; Weyman *et al.* 1995; Duffey 1998; Suter 1999], although variations on the theme are documented [Richter 1970b; Schneider *et al.* 2001]. Since in general, eight threads are observed, it is assumed that the eight silk glands, associated to the frontal spinnerets [*glandulae ampullacea*], are involved in the production of the dragline [Duffey 1998]. Typical for mygalomorphs and web-building labidognatha is the ***dropping*** behaviour [Fig. III.1-2B]. This behaviour involves that a spider climbs up in the vegetation, drops along a drag line and produces in hanging position a second thread which is released in the air. When the latter is long enough, the first is broken down and the spider takes off in the air [Jones 1996a; Suter 1999]. An alternative method consists of behaviour in which the spider drops on one drag line, which is prolonged during the fall. When the thread is again long enough, it breaks at a weak point and aerial dispersal can start [Eberhard 1987]. A third, but mysterious behaviour is foot-basketting, and was only once observed by McKeown [1952, *In*: Jones 1996a]. More information concerning the nature of the silk treads and discussion on the details of the behaviour can be found in Eberhard [1987], Jones [1996a] and Duffey [1994].

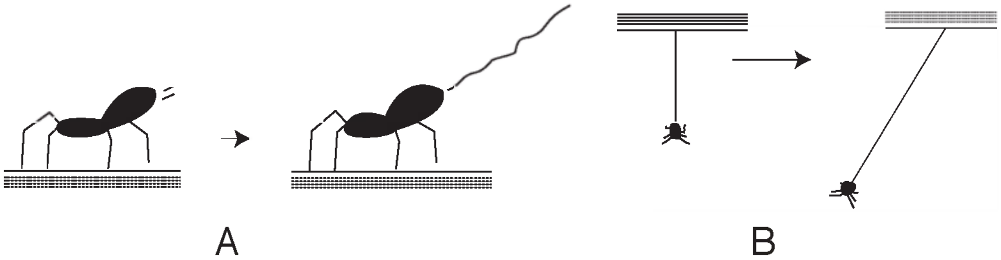

Fig. III.1-2. Schematic representation of the two behavioural mechanisms in preparation of ballooning dispersal [A] tiptoe behaviour [B] dropping behaviour [after Eberhard, 1987].

Benefits of aerial dispersal

Aerial dispersal by means of ballooning is assumed to be an efficient mechanism for long-range dispersal to colonise empty habitats or to escape from habitats with unfavourable environmental conditions as overcrowding, lack of prey or vegetation succession [Toft 1995]. From this point-of-view, ballooning is supposed to occur dominantly in species from unstable and unpredictable habitats [Toft 1995; Duffey 1998]. It is however not restricted to species from these habitats and has also been observed in species from more stable habitats [Richter 1971; Miller 1984; Duffey 1998].

Little direct evidence is however available on long-distance travelling, probably because of difficulties in measuring these [Weyman 1995 and for dispersal in general: Wilson & Thomas 2001]. Although direct observations are scarce and anecdotic [catches of ballooning Linyphiidae at heights of more than 6000 meter [Jones 1996a] and observations of spiders landing on ships 300 km from the nearest coast [Gertsch 1979, *In*: Decae 1987]], they indicate the possibility of spiders to disperse at long distances. At high altitudes, however, temperatures are extremely low and decrease survival chances enormously [Decae 1987]. Moreover if the particular surviving spider is not a fertilised female, chances of colonisation are only possible if conspecific males reach the same location. Certainly in the case of tropical and subtropical regions, ballooning dispersal should be restricted to short-range dispersal, as cold resistance [in case of reaching higher air layers] in these is relatively low [Janzen 1966]. The restriction to short-range dispersal [from a few meters up to several kilometres in case of multiple dispersal events [Thomas *et al.* 2003]] is generally accepted and supported by direct observations [Morse 1993] or modelling work [Thomas 1996; Thomas *et al.* 2003]. Colonisation processes due to long-distance dispersal, although rare, do not depend on mean distances, covered by organisms, but are determined by the exceptional long-distance travellers, situated in the tail of the dispersal curve [Bullock & Clarcke 2000], often following a negative exponential or related equation [Greene & Calogeropoulos 2001].

According to Toft [1995] ballooning dispersal [the author uses the term "*gossamer dispersal*"] is probably bifunctional in agricultural landscapes of the temperate regions, and separated in time. The first function is supposed to be the spread of spiders out of their natal habitat towards suitable microhabitat for maturation and mating and vice-versa. This seasonal dispersal occurs during colder seasons in which meteorological circumstances are less suitable for long-distance travelling [see further]. The second dispersal function takes place during the warm summer season and enables spiders to leave their natal habitat because of the presence of thermal currents and hence higher chances to perform long-distance travelling. In my opinion, these different peaks in aerial dispersal result solely from different meteorological conditions during the species' life cycle and not from different needs of displacement. Weyman *et al.* [2002] confirm this view as these different dispersal peaks were not encountered during a study in Great Britain.

Additionally, indirect studies of spider dispersal through genetic analyses tone down the importance of ballooning for gene flow and hence long-distance dispersal [Ramirez & Haakonsen 1999], although, as mentioned above, genetic analyses should be cautiously interpreted within a dispersal context. Apparently, ballooning is not always an effective dispersal mode between populations and a more stochastic event, certainly in patchily structured populations.

Costs of aerial dispersal

Besides benefits of gene flow and risk spreading in unstable and unpredictable habitats, ballooning dispersal also involves costs. This balance between benefits and costs will finally determine the evolution of spider dispersal rates. Energetic costs, resulting from the production of multiple silk threads and an increased activity [and possibly exposure to less favourable microclimatological conditions *e.g.* higher dehydration rates, prior of the ballooning, by climbing up in the vegetation; Suter 1999] are possible but not yet investigated.

Large costs are associated with the performance of uncontrolled movements in the air current. Besides direct costs by hostile climatological circumstances [Decae 1987] and predation by birds and other predators [Owen & Le Gros 1954; Young & Lockley 1988; Foelix 1996; Robert 1998], the lack of control on the flight direction [Compton 2002] and hence high chances of landing in unsuitable habitat is supposed to be the highest cost. Ballooning dispersal, even if repeated dispersal events are possible, is therefore more an aerial lottery, and especially species, restricted to habitats that are spatially separated will experience a high risk of landing in unsuitable environments [Samu *et al.* 1999; Compton 2002]. If patches are distantly located, low dispersal distances, as a result from low wind velocities [Compton 2002] will complicate successful settling in suitable habitat.

Physical and meteorological determinants of aerial dispersal

A spider, taking-off in the air has to use physical forces, which has to compensate her own body mass. This is only possible within physical constraints and stimulated or restrained by meteorological conditions. As a result, ballooning can not occur in all spiders during the entire season [Humphrey 1987]. According to the latter, ballooning dispersal is constrained by the spider mass and is impossible for spiders weighting more than 32 mg, although exceptionally heavier spiders were already observed to balloon. Illustrative is the observation of ballooning *Stegodyphus dumicola* [Erisidae] of more than 100 mg, but this species used tens of threads [Schneider *et al.* 2001] instead of one. Larger species are also constrained in successful ballooning due to the need of longer preparation periods [longer threads], to take off in the chaotic atmosphere, the presumable higher energetic costs to climb up in the vegetation and the increased chances of predation during the ballooning preparation and the dispersal itself [Suter 1999]. Drag-forces are additionally positively related to the size [and hence mass] of the spider and create as a result an opposing assumption to the possibility of ballooning [Humphrey 1987]. A spider, aiming to balloon in an optimal way has thus to find a balance between mass [not too high] and surface [not too small]. Finally, the maximal length of the thread is constrained by the environment. In complexly structured vegetation, large threads will faster entangle and make ballooning of heavier spiders or long-distance ballooning less probable.

Besides these physical constraints, meteorological conditions determine the success of ballooning in spiders. According to Richter [1970b] and Vugts & Van Wingerden [1976] wind velocities between 0.35 and 1.70 m/s are optimal for ballooning dispersal. If wind velocities are larger than 3 m/s, ballooning is inhibited, probably because of the increased chances of floating away for long distances and hence a high uncertainty of reaching suitable habitat [Humphrey 1987] or by the fact that thermal winds disappear at currents with high velocities [Greenstone 1990]. According to Van Wingerden & Vugts [1974], Greenstone [1990] and Thomas *et al.* [2003], these upwards thermal velocities are necessary because they generate the necessary upwards lift. Because thermal winds are generated by low night temperatures [T_{min}] and high day temperatures [T_{max}] and inhibited by increasing wind speed [<v>], Vugts & Van Wingerden [1974] created the aeronautic index AI=[T_{max}-T_{min}]/<v> which appeared to be a good predictor of ballooning dispersal in their study. Its predicting value was confirmed by Bonte *et al.* [1998] but not by Greenstone [1990].

Other meteorological factors, possibly influencing ballooning behaviour are the amount of sunshine, a vertical gradient in wind velocity [Greenstone

1990] and of course rain [Vughts & Van Wingerden 1974]. Finally, the negative relationship between relative aerial humidity and ballooning frequency, empirical found by Richter [1971] can be explained by the lower density of humid air and hence lower drag forces [Bishop 1990b].

Innate & environmental factors of aerial dispersal

The previously discussed meteorological conditions constrain the effectiveness of ballooning dispersal. According to Vugts & Van Wingerden [1976] and Duffey [1998], they ultimately trigger ballooning dispersal [and the pre-ballooning behaviour]. How these meteorological conditions, and especially the wind velocity, are sensed by the spider remains however unclear. Variation in wind speed can be detected with the trichobotria either directly if the individual is situated in the relevant air layer or indirectly by the detection of vibrations in the vegetation [Weyman 1993]. Other possibilities, although not confirmed nor disaffirmed, are the use of the long silk thread as a sensorial addition, or the presence of baroreceptors [Weyman 1993]. Besides these weather conditions, other environmental factors are known to influence the ballooning dispersal and its initiation. Especially the scarcity of prey, with different threshold levels between sexes and life-stages, is extensively documented as a proximate factor [Legel & Van Wingerden 1980; Duffey 1994; Weyman & Jepson 1994; Duffey 1998; Bonte & Maelfait 2001; Weyman *et al.* 2002]. Seasonal variation and day/night variation are also documented as proximate mechanisms. They can, however, respectively be related to variation in the population density or relative prey availability [Toft 1995; Weyman *et al.* 1995] and the lack of optimal meteorological conditions at night [Weyman 1995]. If meteorological conditions during the night are optimal, ballooning dispersal, however, can occur, as observed in Australia [Farrow 1986].

One of the main possible innate factors is the genetic basis of the ballooning propensity, although not yet documented. Variation within species [Richter 1970; Miller 1984] and within populations [Richter 1971] suggest that natural selection is responsible for the large variation in dispersal propensities and methodologies [see higher]. Little experimental work has been carried out on factors underlying the initiation of ballooning behaviour, or on genetic variance underlying phenotypic variation [Weyman 1993]. Only Li & Margolies [1993] found additive genetic variation for ballooning behaviour in the related two-spotted spider mite, *Tetranychus urticae*. In the latter study, however, nonadditive genetic variation and maternal effects or common environmental variation explained the largest part of the phenotypic variation, and covariation with fecundity and sex ratio was found; the residual variance during the experiments was minimised to 43-60%. This large source of residual variance is a major problem in estimating heritability of behavioural traits, resulting from their low level of repeatability caused by difficulties in keeping experimental conditions or the individual's internal state constant [Kecic & Marinkov 1974].

In general, ballooning is restricted to smaller individuals, hence juveniles in the families of larger species and to adults and juveniles in the money spiders Linyphiidae. This age-effect may be an effect of mechanical constrains [mass; see higher], but species-specific patterns in the Linyphiidae [dominant adult or juvenile dispersal, according to the species] lead to the hypothesis of the existence of species-specific internal clocks [Duffey 1998]. This timing is probably strengthened or weakened by proximate environmental conditions. Age-specific foraging strategies can also be related to age-related intraspecific differences in ballooning propensity [Kevan & Greco 2001].

A difference in ballooning dispersal between the sexes is a mechanism to avoid inbreeding and mate competition [Massot & Clobert 2000]. Deviations from an equal sex-ratio are commonly observed under field conditions, but may reflect differences within the population [Bonte *et al.* 1998]. Schneider *et al.* [2001] found a dominance of females in ballooning Eresidae. According to Thomas & Jepson [1999], this female dispersal can be interpreted as a form of risk spreading in which females search for places to deposit eggs in different environments ["bet hedging" strategy: Vepsalainen 1978]. Maternal effects through the maternal condition, resulting in differences in egg quality, also potentially influence ballooning dispersal, as shown for ballooning in caterpillars [Diss *et al.* 1996]. In spiders, however, no evidence of maternal condition effects has been found. Direct effects of population density [Turnbull 1973; Legel & Van Wingerden, 1980 & Weyman *et al.* 1995] and interspecific cannibalistic interactions [Fox 1975] also have been suggested to influence ballooning rates, but until now, these effects has not been separated from covarying prey limitation. Different thresholds of offspring to perform the dispersal behaviour are in accordance with the previously mentioned "random" mixed ESS [Parker & Stuart 1976]. This apparently "random" strategy may hence be a cryptic environmental or evolutionary trigger that only appears to be random because of hardly detectable relationships with the [genetical] environment.

Research on spider dispersal in coastal grey dunes

As illustrated in the previous general introduction, and highlighted by Nathan [2001], the knowledge of dispersal evolution, motivation, its effect on metapopulation dynamics and species distribution at multiple scales is poorly understood and many questions remain unsolved or empirically unverified. In this part of the thesis we aim to contribute to the knowledge of dispersal, by studying both ecological and evolutionary aspects of spider dispersal in fragmented grey dunes. Studies were performed at the individual, population and assemblage level. In the study of the influence of ballooning dispersal on population dynamics and the distribution of species, we assumed a random dispersal pattern within air currents, as wind directions with velocities of <3 m/s are not directional in one year [year 2000: angular dispersion r= 0.13; P=0.39; Fig. III.1-3] and especially variable during days with very low wind velocities [Data from Meteorologische Berichten KMI 2000].

Spiders from grey dunes were used as model organisms, and genotypic and phenotypic variation in dispersal were studied in detail for two model species. *Erigone atra* [Blackwall, 1841], a common species performing a high *tiptoe* performance, was selected to study the contribution of genetic and different environmental effects during the juvenile development and the adult life stage on the latency of the pre-ballooning behaviour because of its fast generation time, easy breeding possibility and high ballooning frequencies [De Keer & Maelfait 1988a,b]. Field experiments on variation in cursorial dispersal and common garden experiments in the laboratory on ballooning behaviour were investigated in the wolf spider *Pardosa monticola* [Clerk, 1757]. This species was chosen because of its high abundance in fragmented grey dunes, its high observability and trapability, and the fact that females attach their egg sac and early-juvenile offspring on the abdomen [Bonte & Maelfait 2001]. As these juveniles are the potential ballooners, interdemic and geographic variation could easily be studied in the lab by excluding direct environmental effects. Tiptoe-behaviour was observed in a test chamber, following Legel & Van Wingerden [1980]. Spiders were individually placed on a plastic frame or in groups of maximal five individuals [in case of laboratory reared juveniles of *Pardosa* species] on a platform, placed in an air tunnel with upward currents at a temperature of 30 ±2°C, aerial humidity of 40-50% and a light breeze – velocity 1-1.2 m/s. To prevent the spiders from escaping by walking, the frame or platform was placed in a bath of water [see Fig. III.1-4].

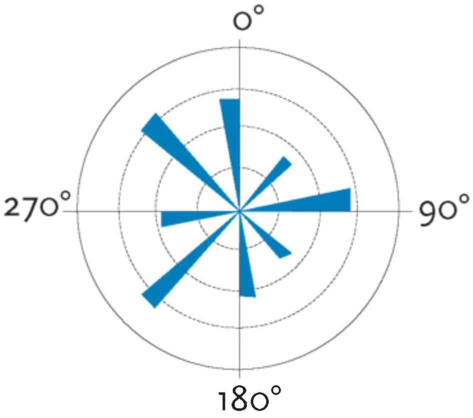

Fig. III.1.-3. Distribution of wind direction with velocities lower than 3 m/s throughout the year 2000. Data from Koksijde Meteorologisch Station [2°39'NB; 51°05' WL -[Meteorologische Berichten KNMI 2000].

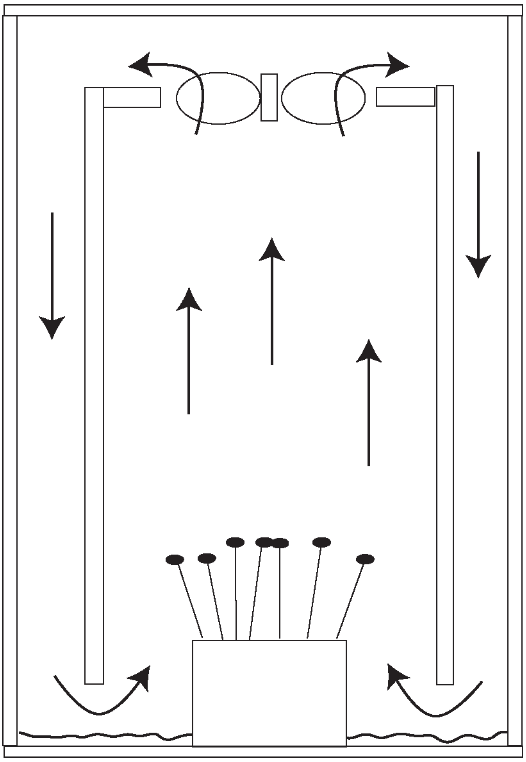

Fig. III.1-4. Schematic representation of the used test chamber for the observation of tiptoe-behaviour in spiders [here with platform, as used in the Pardosa monticola-experiment, described in chapter III.6 [Picture by Jeroen Vanden Borre].

In the first two chapters, we report on patterns of interspecific variation in ballooning dispersal and its effect on the species' distribution. The ballooning propensity of 29 species, occurring in grey dunes along the Flemish coast was tested under standardised laboratory conditions. As macro-selection should benefit a well-developed ballooning behaviour if the risk of landing in an unsuitable habitat is lower than the probability in reaching a suitable habitat, we investigated its relation to the degree of habitat specialisation and hypothesised that specialised species would be characterised by lower dispersal propensity than generalists [**chapter III.2**]. The same dataset of spider ballooning propensity was used to study the importance of ballooning dispersal versus the degree of habitat specialisation and the landscape configuration in shaping species distribution patterns [**chapter III.3**]. The latter were derived from pitfall sampling campaigns of 19 grey dune patches.

In **chapter III.4**, we aimed to disentangle the relative contribution of prenatal environmental [maternal], genetic and postnatal environmental effects [different breeding conditions and acute starvation] on the ballooning latency of the common *Erigone atra*. Offspring of several families were reared under different breeding conditions, enabling us to analyse variation in pre-ballooning behaviour in a quantitative genetic way, by genotype x environment [GxE] interactions. Repeatability of this behaviour was additionally investigated within a methodological framework for future research.

In the last part, the contribution of both aerial and cursorial dispersal in metapopulation dynamics of the dune wolf spider *Pardosa monticola* and interdemic [and geographical] variation in both dispersal modes were studied within a fragmented dune landscape with patches of different quality. In **chapter III.5**, we investigated general patterns in population dynamics of the dune wolf spider *P. monticola* and the relative importance of cursorial and aerial dispersal for patch colonisation and extinction. Patch occupancy patterns were studied during two years and patch dynamics were investigated by the application of an incidence function model in which patch quality and connectivity were included as independent variables. Population-genetical variation was additionally studied by allozyme electrophoresis. Because this model-approach only reveals general patterns and indirect evidence of the importance and dispersal, variation in aerial dispersal was studied more into detail in function of the landscape and the maternal habitat [***chapter III.6***]. As females were sampled from landscape with different degrees of grassland configuration, we hypothesised that, due to increased costs of floating out of suitable habitat, offspring dispersal would be highest in the open, large dune landscape and lowest in the isolated and closed landscape with a small area of suitable grassland habitat. Intraspecific variation was additionally investigated within four subpopulations in the Flemish coastal dunes and linked to features of habitat predictability and maternal condition.

Finally, emigration of *P. monticola* by means of cursorial dispersal was studied in three grasslands from different quality by pitfall trapping and by direct observations on orientation behaviour at different distances from the patch edge, within the moss-dune matrix [***chapter III.7***].

III.2

LOW PROPENSITY FOR AERIAL DISPERSAL IN SPECIALIST SPIDERS FROM FRAGMENTED LANDSCAPES

FOTO: WWW.ARACHNOLOGY.ORG

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Abstract

Aerial dispersal by ballooning is a passive flight, by which wind dragging generates an upward lift on a silk thread. It is likely to reflect an aerial lottery, in which the absence of flight direction control is a serious cost for long-distance dispersal in a fragmented landscape. For species, occurring in one patchily distributed habitat type, dispersal should evolve in a different way than morphological traits, directly linked to active dispersal. Therefore, we expect that, if the risk of landing in an unsuitable habitat is lower than the probability in reaching a suitable habitat, selection should benefit a well-developed ballooning behaviour. We investigated interspecific variation in the ballooning-initiating tiptoe behaviour as it is linked to spider dispersal performance. Our results indicate indeed that ballooning performance is negatively related to habitat specialisation in spiders from patchy grey dunes, so habitat specialists are characterised by poorly developed dispersal behaviour. These findings are concordant with recent insights that dispersal is selected as risk spreading in generalists, while it is selected against in specialist species.

Keywords: evolution, dispersal, habitat specialisation, phylogenetical background

Introduction

Dispersal in wingless arthropods occurs via passive transport in air currents, so called ballooning if silk threads are used. Ballooning is known from many arthropod groups and initiated by behavioural adaptations that enable the individual to take-off in the air. Spiders will initiate tiptoe behaviour, an observable behaviour by which the legs are stretched and the abdomen is raised before the silk thread is produced from the spinnerets. Ballooning is especially known from a large variety of spider families *Araneae* [e.g. Salmon & Horner 1977; Dean & Sterling 1985] and restricted to the juvenile instars from the larger species due to physical constraints [Humphrey 1987]. It is triggered by innate responses on acute food shortage [Weyman & Jepson 1994] or on food shortage during the juvenile development [Bonte *et al*. 2003b]. Developmental temperature also explains a substantial part of the observed individual variation [Bonte *et al*. 2003b]. Additionally, environmental factors influence the ballooning propensity [Weyman 1995]. In the field, effective take-off only occurs during suitable meteorological conditions [Richter 1970; Van Wingerden & Vughts 1974; Greenstone 1990; Duffey 1998]. Especially high air temperatures and low wind velocities [<3 m/s] are important for the initiation of ballooning dispersal [Vughts & Van Wingerden 1976].
Although factors as climbing up in the vegetation and taking-off are important factors that influence the effective aerial dispersal [Weyman 1993], studies on the latency to initiate tiptoe behaviour are important for understanding variation in the willingness of the spider to disperse by ballooning under suitable meteorological conditions, since it is only expressed in advance of aerial dispersal [Weyman 1993]. Especially the fact that ballooning proportions are constant during several tiptoe observation tests [Richter 1970] stresses the reliability of measuring variation in the performance of ballooning-initiating behaviour within a dispersal framework.

Ballooning is supposed to be an efficient mechanism for distant dispersal and hence for colonisation of suitable but unoccupied habitats [Toft 1995; Duffey 1998]. Recent empirical investigation failed however to prove the importance of ballooning in short-term colonisation processes, although it was the best predictor explaining the patch occupancy, resulting from long-term colonisation and extinction dynamics [Bonte *et al.* 2003c]. Indirect studies of ballooning dispersal also tone down the importance of ballooning for gene flow [Ramirez & Haakonsen 1999]. Apparently, ballooning is not always an effective dispersal mode between populations and a more stochastic event, certainly in patchily structured populations.

Since passive aerial dispersal depends on air currents, wind directions and body mass, and dispersing individuals have no control on the flight direction [Compton 2002], ballooning dispersal is more a lottery. In heavily fragmented landscapes, suitable habitats are patchily distributed within an unsuitable matrix. Especially for species from these fragmented habitats, aerial dispersal should involve a high risk in reaching potential suitable habitats [Samu *et al.* 1999; Compton 2002]. If patches are distantly located, low dispersal distances, as a result from low wind velocities [Compton 2002] additionally complicate successful colonisation.

Theoretical studies on the evolution of dispersal revealed that it is selected against by intrinsic costs and stable environmental heterogeneity [Holt 1985; Doebeli & Ruxton 1997; Doebeli & Ruxton 1998; Parvinen 1999; Mathias *et al.* 2001], while it is favoured by kin competition [Hamilton & May 1977; Perrin & Lehman 2001; Lehman & Perrin 2002], inbreeding depression [Chesser & Ryman 1986; Perrin & Mazalov 1999; Perrin & Mazalov 2000] and temporal variability in habitat quality [Van Valen 1971; McPeek & Holt 1992]. Recently, Kisdi [2002] found that risk spreading in stochastic environments and adaptation to permanent properties of local habitats interplay in the simultaneous evolution of dispersal and habitat specialisation. Roff [1981] analysed the relative costs and benefits of wind dispersal and Van Valen [1971] emphasised the trade-off between passive aerial dispersal and competitive abilities. Other authors [*e.g.* Roff 1975; Den Boer 1981; McLachlan 1985; McPeek & Holt 1992] hypothesised and confirmed that the advantages of well-developed dispersal abilities decline in stable and homogeneous habitats. Species inhabiting one fragmented habitat type should be characterised by similar ballooning behaviour propensities. Interspecific differences have however been observed [Van Wingerden 1980; Greenstone 1982; Miller 1984], so additional evolutionary processes must have generated this variation of the dispersal-linked behavioural trait.

Because of the apparent large cost of passive aerial dispersal in fragmented landscapes, we expect positive selection for the performance of the ballooning dispersal if the individual benefits from the dispersal. Natural selection should reduce a well-developed ballooning behaviour, if the risk of landing in an unsuitable habitat is high or if the species is strictly specialised to one [heavily fragmented] habitat type. Patterns of selection for reduced dispersal have been observed for wind-dispersed seeds in isolated plant populations [Carlquist 1966; Cody & Overton 1996]. Selection for dispersal in generalists hence favours risk spreading because of a suboptimal adaptation to the local habitat, while dispersal is selected against in specialists by adaptation to local environmental conditions [Kisdi 2002].

Vegetation of grey dunes includes Atlantic moss dominated dunes [mainly *Tortula ruralis*] as well as dune grassland [with a distinct organic soil layer] belonging to the *Cladonio-Koelerietalia* in case of lime rich grey dune and to the *Trifolio-Festucetalia ovinae* in case of decalcified grey dunes [Provoost *et al.* 2002]. Climatological conditions are extreme with high temperature and low humidity in the summer. As a result, arthropod abundance peaks during winter and spring [Bonte *et al.* 2000a; Bonte *et al.* 2002d]. Patch quality and isolation are the main determinants explaining population dynamics of a typical spider species [Bonte *et al.* 2003c]. In order to test the prediction of a reduced dispersal propensity in specialised species, showing strong morphological, behavioural and phenological adaptation to this habitat type, we relate experimental data on the performance of ballooning behaviour by grey dune spiders to their degree of their habitat specialisation.

Methods

Study organisms: collection and testing instars

Between April 1999 and May 2001, spiders were collected from grey dune vegetation from the coastal dunes in De Panne and Oostduinkerke [Belgium]. Dwarfspiders [Linyphiidae], *Argenna subnigra* [Dictynidae], *Zelotes electus* [Gnaphosidae], *Ozyptila simplex* [Thomisidae] and *Hypsosinga albovittata* [Araneidae] were sampled by collecting moss and low-herb vegetation and manual extraction in the lab. Egg sacs [guarded by the female] of *Xysticus* species [Thomisidae] were searched during April-June in the moss vegetation and reared in the lab on petri-dishes with plaster of Paris under room temperature and an aerial humidity near to saturation. Wolfspiders [*Lycosidae]* with an attached cocoon or with juveniles on the back were actively collected by hand [for species of the genus *Pardosa* and *Arctosa perita]* or passively by using dry pitfalls [for species of the genus *Alopecosa*]. The pitfalls were emptied every three days during a two-week period in April-May 1999 [for species of the genus *Alopecosa*]. Hand collections were performed in March [*A. perita*] and June-July for *Pardosa* species. Juveniles were reared in the lab under the same conditions as *Xysticus* spiderlings until the second or third instars [Collembolan *Isotoma viridis* as prey ad libitum].

Only adult dwarfspiders *Linyphiidae* and small juvenile spiders from the other genera were used for the experiment, since these have ideal masses for aerial dispersal [< 1mg: Greenstone *et al.* 1987]. If possible, individuals were tested in the moulting instars in which they were already encountered as ballooning individuals in field situations [instar II,III for Lycosidae and Thomisidae, instar III –subadult for *Argenna subnigra* and *Hypsosinga albovittata*; Bonte *et al.*, 1998; Bonte & Maelfait 2001].

Estimating ballooning propensity

The propensity to express tiptoe behaviour was tested following Legel & Van Wingerden [1980] and Bonte *et al.* [2003b]. Spiders were individually placed on a plastic frame or in groups of maximal five individuals [in case of laboratory reared juveniles of *Pardosa* species] on a platform, so intraspecific interactions were reduced. Recorded ballooning frequencies were similar in both testing designs [Bonte, unpub. data], so data from all experiments could be used in the same analysis. The testing platform or frame was placed in an air tunnel with upward currents at a temperature of 30 ±2°C, aerial humidity of 40-50% and a light breeze – velocity 1-1.2 m/s. To prevent the spiders from escaping by walking, the frame or platform was placed in a bath of water.

Observations were conducted during 20 minutes. Only if the tiptoe behaviour persisted for at least three seconds, the observation was interpreted as valid [Bonte *et al.* 2003b].

Since nutritional conditions influence the ballooning behaviour [Bonte *et al.* 2003b] and more specifically starvation acts as the final trigger for the initiation of the tiptoe behaviour, spiders were fed in the lab at libidum with *Isotoma viridis* [Collembola] and starved for one week, before testing in the experimental chamber.

Estimation of habitat specialisation

Species-specific levels of habitat specialisation were estimated in two ways: By using the level of maximal indicator value in the dichotomous and hierarchical clustering of the pitfall data from all kinds of coastal dune vegetation [as documented in Bonte *et al.* 2002a] as an approach of eurytopicity [Dufrêne & Legendre 1997]. This approach determines indicator species at different hierarchical or non-hierarchical levels of clustering by combining relative species abundance with its relative frequency of occurrence in the various groups of site within each level of clustering. Species with a maximal indicator value [IndVal] at the first level are generalist eurytopic species in the dune area, occurring in many kinds of dune vegetations; those with maximal IndVal at the lower level [level 6] occur only in very specific habitats [grey dune] and are specialised stenotopic species. Species with a maximal IndVal at intermediate division levels are bound to more than one type of typical coastal dune habitat. Dispersing individuals accidentally trapped in a certain habitat will only marginally influence the IndVal calculation due to its specific algorithm [Dufrêne & Legendre 1997].

By counting the number of distinct habitat types, as given by Hänggi *et al.*

[1995], in which species were regularly found in Central Europe. The negative logarithms were taken to scale this measurement normally in the same way as the previous estimate.

Statistical analyses

Data on individual tiptoe performance were used as binomial response variables in a generalized mixed linear model with logit link [glimmix procedure in SAS 8.1], with backwards elimination of non-significant variables. Habitat specialisation was included as a continuous factor.
Phylogenetical background was included as fixed factor. For our tested species, however, only two parallel clades are currently distinguished [Coddington & Levi 1991]: Orbicularia [including Araneidae, Linyphiidae, and Tetragnatidae] and the RTA-clades [including Gnaphosidae, Dictynidae, Thomisidae and Lycosidae].
Species was included as random factor and tested against the χ^2 distribution [df=1] of the Log-Likelihood-difference between the models with and without random factor.

Results

Relation between habitat specialisation and ballooning frequency

The species used for the experiment and the numbers of tested individuals are given in Table III.2-1. The ballooning frequency differs between species and depends on the degree of habitat specialisation and phylogenetical background. Variation explained by the random factor [species] is significant for the IndVal [σ^2=0.827; χ^2_1=287.1; p<0.001] and the Hänggi approach [σ^2=1.094; χ^2_1=95.5; p<0.001].

IndVal habitat specialisation is negatively related with the ballooning frequency [model slope of -0,732 ± 0,127] and interacts significantly with the phylogenetical background in case of the Hänggi habitat specialisation [Table III.2-2]. Here, model slopes are –1.027 ± 0.261 [s.e.] and –0.397 ± 0.313 [s.e.] for respectively the Orbicularia and RTA-clades. Phylogenetical

Species and family	**IndVal-level**	**# habitat types**	**ball. freq. %]**	**n**
Alopecosa barbipes [Sundevall, 1833] [Lycosidae]	3	19	8.95	67 [6]
Alopecosa fabrilis [Clerck, 1757] [Lycosidae]	6	8	0.00	21
Alopecosa pulverulenta [Clerck, 1757] [Lycosidae]	2	72	16.36	55 [4]
Arctosa perita [Latreille, 1799] [Lycosidae]	2	12	20.91	110 [7]
Argenna subnigra [O.-P. Cambridge, 1861] [Dictynidae]	1	16	40.00	35
Centromerita concinna [Thorell, 1875] [Linyphiidae]	2	38	56.37	55
Erigone atra Blackwall, 1833 [Linyphiidae]	1	79	96,000	300
Erigone dentipalpis [Wider, 1834] [Linyphiidae]	2	76	73.21	56
Hypsosinga albovittata [Westring, 1851] [Araneidae]	3	16	33.33	15
Meioneta rurestris [C.L. Koch, 1836] [Linyphiidae]	2	85	77.50	40
Ozyptila simplex [O.P.-Cambridge, 1862] [Thomisidae]	2	25	32.35	34
Pachygnatha degeeri Sundevall, 1830 [Tetragnathidae]	2	75	35.59	59
Parapelecopsis nemoralis [O.P.-Cambridge, 1884] [Linyphiidae]	2	12	10.57	123
Pardosa monticola [Clerck, 1757] [Lycosidae]	4	16	8.08	569 [22]
Pardosa nigriceps [Thorell, 1856] [Lycosidae]	1	31	42.26	97 [6]
Pardosa pullata [Clerck, 1757] [Lycosidae]	2	67	15.73	89 [7]
Pelecopsis parallella [Wider, 1834] [Linyphiidae]	5	47	20.59	34
Styloctetor romanus [O.P.-Cambridge, 1872] [Linyphiidae]	6	1	12.69	134
Tenuiphantes tenuis [Blackwall, 1852] [Linyphiidae]	1	77	85.29	34
Thyphochrestus digitatus [O.P.-Cambridge, 1872] [Linyphiidae]	5	16	10.95	210
Tiso vagans [Blackwall, 1834] [Linyphiidae]	3	56	46.87	32
Trichopterna cito [O.P.-Cambridge, 1872] [Linyphiidae]	3	16	22.99	87
Walckenaeria monoceros [Wider, 1834] [Linyphiidae]	2	14	45.83	48
Walckenaeria stylifrons [O.P.-Cambridge, 1875] [Linyphiidae]	6	3	4.35	23
Walckenaeria antica [Wider, 1834] [Linyphiidae]	1	59	88.23	34
Xysticus kochi Thorell 1872 [Thomisidae]	3	43	32.31	65 [3]
Xysticus ninnii [Thorell, 1872] [Thomisidae]	5	6	0.00	21 [1]
Xysticus sabulosus [Hahn, 1832] [Thomisidae]	4	6	13.64	110 [6]
Zelotes electus [C.L. Koch, 1839] [Gnaphosidae]	2	16	36.00	25

Table III.2-1 - Species that were tested for tiptoe behaviour, with indications of their degree of habitat specialisation [IndVal level from Bonte et al. 2002a; number of habitat types in which the species occurs following Hänggi et al. 1995], observed ballooning frequency and number of tested individuals [with notes on the number of mothers in case of laboratory rearing]

background only explains significant variation in case of the IndVal-model and does not interact with the degree of habitat specialisation [Table III.2-2]. Model parameter estimates for the RTA and Orbicularia clade are in this case respectively 1.076 ± 0.442 [s.e.] and 0.495 ± 0.432 [s.e.].

The goodness of the models [Fig. III.2-1] is significant [$\chi_{\text{indVal}}{}^{2}{}_{2560}=2011.94$; $\chi_{\text{Hänggi}}{}^{2}{}_{2559}= 2011.14$; both $p<0.0001$] and standardised residuals are normally distributed [Shapiro Wilk's $W_{\text{IndVal}}=0.97$ and $W_{\text{Hänggi}}=0.96$]

Table III.2-2 - Results of logistic model for ballooning frequency with habitat specialisation [HabSpec for both IndVal and Hänggi approach] and phylogenitical background [Phyl] as dependant variables.

Specialisation approach	**Variable**	**numerator d.f.**	**denominator d.f.**	**F**	**p**
IndVal	HabSpec	1	32.1	33.00	<0.0001
	Phyl	1	27.3	15.68	0.0005
	Phyl*HabSpec	1	34.5	1.06	0.311
Hänggi	HabSpec	1	27.4	14.35	0.0008
	Phyl	1	27.8	0.23	0.636
	Phyl*HabSpec	1	25.5	8.05	0.0080

Discussion

The present laboratory study demonstrates that spider species, characterised by a high degree of habitat specialisation show lower ballooning propensities than species occurring in a wide variety of habitats.

In general, ballooning dispersal is thought to be more common in species from unstable and ephemerous habitats [like arable land], which become quickly unsuitable [Samu *et al.* 1999]. Apparently ballooning dispersal seems to be evolved in the same way as flight ability in winged insects [*e.g.* Roff 1975; Den Boer 1981; McLachlan 1985]. Some authors confirm differences in ballooning frequency between species [Van Wingerden 1980;

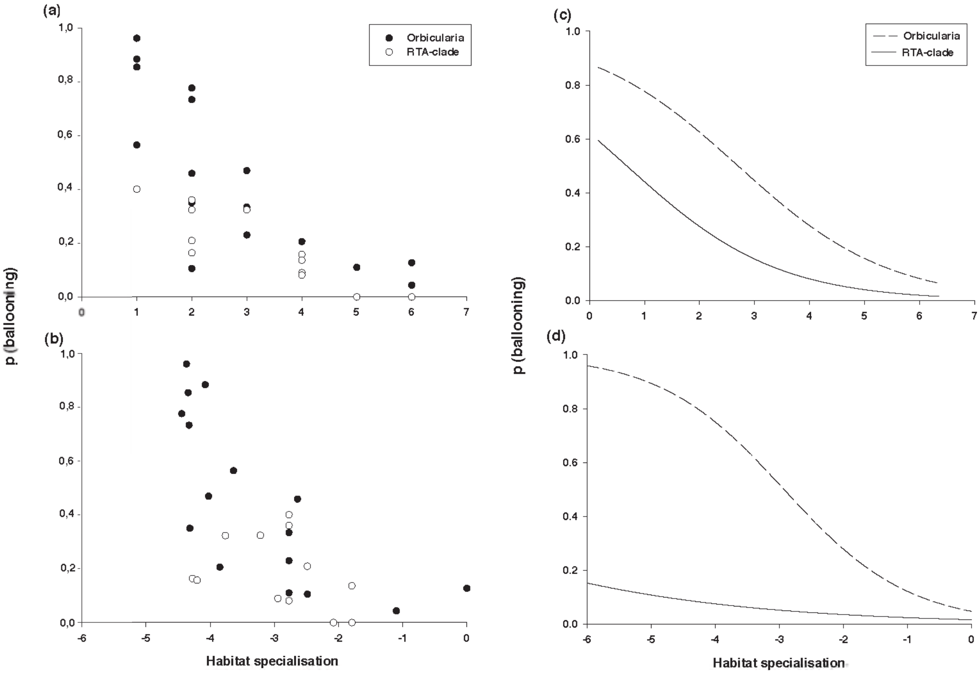

Fig. III.2-1: Relation between ballooning propensity and the degree of habitat specialisation in grey dune spiders from the RTA-clade and the Orbicularia.
[a] Mean species frequency and [c] logistic model for habitat specialisation as derived from IndVal levels [Bonte et al. 2002a], [b] Mean species' frequency and [d] logistic model for habitat specialisation as derived from Hänggi et al. [1995].

Greenstone 1982; Miller 1984], but intraspecific differences are not yet documented, although Bonte *et al.* [2003b] found genetic variation at the basis of the ballooning-initiating behaviour.

Our data suggest that variation in the pre-ballooning behaviour for species from one habitat type in a heterogeneous landscape is related to their degree of habitat specialisation and phylogenetical background.
In addition to earlier findings of Richter [1970,1971] our results indicate that the evolution of this behavioural trait, linked to dispersal, originates additionally from other factors than the nature [stability] of the habitat

[Southwood 1977]. The ability of the species to survive in other habitats is apparently an important determinant of ballooning evolution in fragmented habitats within heterogeneous landscapes. Similar results on reduced dispersal in patchy habitats have also been found in specialised cactophilic *Drosophila* species from Central-American deserts [Markow & Castrezana 2000].

For eurytopic species, able to survive in many habitat types, the cost of ballooning is certainly lower than for specialised species and a well-developed ballooning behaviour is evolutionary favoured. As already predicted by theoretical models [Kisdi 2002], dispersal propensity in spiders from grey dunes is selected as risk spreading in generalist species, while it is selected against in specialist species, the latter being adapted lo local habitat conditions. Since only species from one habitat type were investigated, differences in habitat stochasticity cannot act as a selector for dispersal. Data on the population genetic structure are only available for one species with an intermediate degree of habitat specialisation [*Pardosa monticola*: Bonte *et al.* [2003c]] and indicate a very low genetic differentiation between even very distant populations. Other studies on coastal dune arthropods confirm this low differentiation [Ramirez & Froehlig 1997; Boulton *et al.* 1998], suggesting similar environmental selection pressures [sand overblowing]. Additionally, spider densities are very high [Bonte *et al.* 2000a], so kin competition and inbreeding depression are less likely to select for dispersal. This new insight possibly explains surprisingly high ballooning proportions in spiders from stable habitats [Miller 1984]. Reduced dispersal by short-term selection has also been observed for wind-dispersed seeds in isolated plant populations [Carlquist 1966; Cody & Overton 1996].

Phylogenetical background, in which species from the Orbicularia perform a better ballooning behaviour in comparison to species from the RTA-clade explains substantial amount of the observed variation. Dependant of the used measurement of habitat specialisation, phylogeny is significant on its own or in interaction with habitat specialisation. Different patterns in the approach of habitat specialisation [IndVal levels have a much narrower range than the direct counts from Hänggi *et al.* [1995]] originate this contrast, although the two used measurements correlate well. Species from the Orbicularia show in both cases higher or equal ballooning propensities for a given degree of habitat specialisation. This clade contains orb and cobweb spiders [Coddington & Levi 1991], species living in the higher strata of the vegetation and dependant of a well-developed silk production for web building. Their occupancy of patches of taller vegetation and the more frequent silk production probably increase the number of opportunities for ballooning. Many species of this clade are also small-sized [Linyphiidae] in the adult stages, and can physically balloon during their entire life cycle, this in contrast to the larger species [more represented in the RTA-clade] in which ballooning is only restricted to the [early] juvenile instars. This may additionally strengthen selection for dispersal. An interaction or covariation between morphological and behavioural evolution, related to dispersal, is thus observed. As only the phylogenetical clade separation is currently available, a considerable amount of variation explained by the degree of habitat specialisation may actually result from weaker phylogenetical relationships rather than from habitat association per se. However, the effect of specialisation is clear within related species from the same family [Lycosidae and Linyphiidae] and within species from the same genus [*Alopecosa, Pardosa, Xysticus, Wlackenaeria*], indicating a true effect of the degree of habitat specialisation.

A well-developed dispersal capacity is the first condition for a successful colonisation [Den Boer 1970; Thomas *et al.* 2001b; Bullock *et al.* 2002] and is related to local distribution [Malmqvist, 2000] or patch occupancy in fragmented habitats [Hanski 1999a]. Effective wind dispersal has already been strongly linked to colonisation ability in a number of plant species [Grime 1986; Dwzonko & Loster 1992; Nakashizuka *et al.* 1993; Stöcklin & Bäumler 1996]. Ballooning in spiders has also been shown to be effective in the colonisation of recently cleared land [Meijer 1977; Weyman & Jepson 1994] and explains occupancy patterns of species [Bonte *et al.* 2003c]. Our data suggest that in fragmented habitats, spider dispersal propensity declines in habitat specialists. As a result, habitat specialists wwill be exposed to higher extinction chances than their more eurytopic conspecifics. So, intrinsic rare species will become rarer due to reduced dispersal if fragmentation increases.

III.3 EFFECTS OF AERIAL DISPERSAL, HABITAT SPECIALISATION, AND LANDSCAPE STRUCTURE ON SPIDER DISTRIBUTION ACROSS FRAGMENTED GREY DUNES

FOTO: DRIES BONTE

BONTE D., BAERT L., LENS L. & MAELFAIT J.-P. *Ecography*, in press.

Abstract

Species distribution patterns have been explained by Hutchinson's niche theory, metapopulation theory and source-sink theory. Empirical verification of this framework, however, remains surprisingly scant. In this paper, we test the hypothesis that landscape characteristics [patch size and connectivity], aerial dispersal ability and niche breadth interact in explaining distribution patterns of 29 spider species inhabiting fragmented grey dunes. Distribution patterns only depended on aerial dispersal potential, and the interaction between patch connectivity and area. Niche breadth, measured as the degree of habitat specialisation in the total coastal dune system, did not contribute to the observed distribution patterns. Additional variation in patch occupancy frequency was strongly species-dependent and was determined by different responses to the degree of patch connectivity for ballooning dispersal. Results from this study suggest that dispersal ability largely affects our perception of a species 'fundamental niche', and that source-sink and metapopulation dynamics may have a major impact on the distribution of species. From a conservation point of view, specialised [and hence intrinsically rare] species can be predicted to become rarer if fragmentation increases and connectivity decreases. This study is, to our knowledge, one of the few linking species distribution [and not patch occupancy, species diversity or richness] to landscape ecological [patch connectivity and area] and auto-ecological [niche breadth, dispersal potential] features.

Keywords: Araneae, ballooning, metapopulation, niche, source-sink

Introduction

Hutchinson's niche theory, metapopulation theory and source-sink theory combined, provide a solid conceptual framework for the study of species distribution patterns [Pulliam 1988, Hanski 1998, 1999a, 1999b, Pulliam 2000]. Empirical verification of this framework, however, remains surprisingly scant [Pulliam 2000]. Besides, case studies examining the effects of organism-based parameters and landscape structure on distribution patterns often yield inconsistent results. For instance, species regularly prove absent from 'suitable habitat' [as predicted by the modified Hutchinson's *n*-dimensional niche concept; Hutchinson 1957] and present in 'less suitable' one [Pulliam 2000].

Patterns of distributions in heterogeneous landscapes thus reflect complex biotic interactions, such as between species competition, dispersal, niche breadth and the distribution of environmental parameters in space and time [e.g. Pulliam & Danielson 1991; Moilanen & Hanski 1995; Pulliam 2000]. Metapopulation theory states that local population extinctions are not as uncommon as previously thought [Brooker & Brooker 2002, Smith and Hellmann 2002] and may result from stochastic changes in habitat quality and demography combined with poor ability of dispersal [Hanski 1998]. The latter has been widely identified as a key process in both population regulation and spatial distribution in plants and invertebrates [*e.g.* Malmqvist 2000; Thomas 2000; Johnson *et al*. 2001; Verheyen & Hermy 2001; Hedenas *et al*. 2003]. Yet, other studies have failed to demonstrate clear-cut relationships between dispersal and distribution [*e.g.* Andersson *et al*. 2000; Malmqvist 2000; Clarke *et al*. 2001; Rundle *et al*. 2002] or have revealed counterintuitive patterns [e.g. Guitiérrez & Menéndez 1997]. Habitat fragmentation may both promote and reduce mobility, depending on the degree of resource or habitat specialisation [Wiens 2001]. Thus, ecologically related species occupying the same environment may differ markedly in their responses to landscape change and fragmentation, depending on how dispersal and niche breadth are expressed in their respective populations, possibly as a result of local adaptation. Moreover, levels of habitat specialisation and of dispersal ability have been previously shown to be interrelated in spiders from fragmented grey dune habitats [Bonte *et al*. 2003c].

Despite the above, few studies have attempted to integrate species-level and landscape-level variables to explain patterns of species distribution [Thompson *et al.* 1999] or patch occupancy [Lens *et al.* 2002]. We apply such approach to study the distribution of spider [*Araneae*] species across a network of grey dune patches along the Belgian coast. Due to increased urbanisation for tourist facilities, the total area of dune habitat in Belgium has decreased from 6000 ha to less than 3800 ha since the beginning of the 20th century, and became increasingly fragmented [Vermeersch 1986]. In addition, local farmers started to abandon their agropastoral activities after the Second World War, resulting in a steady increase of Sea Buckthorn-shrubs *Hippophae rhamnoides*. This, in combination with a crash of the rabbit population *Oryctolagus cuniculus* due to viral diseases myxomatosis and VHS, lead to a further reduction and fragmentation of grey dune vegetation [Provoost *et al.* 2002]. An earlier survey of spider species in remaining grey dune fragments revealed a positive relationship between presence of typical grey dune species and patch size [Bonte *et al.* 2002a]. Such a relationship may both reflect poor colonization ability, high sensitivity to environmental stress, or interactive effects between these [and other] variables. In this paper we test the hypothesis that characteristics at landscape level [patch size and isolation] and population level [dispersal ability and niche breadth] interact when affecting distribution patterns of spiders in a heterogeneous and severely fragmented coastal dune landscape.

Material and methods

Study area and species

Fieldwork was conducted in the Flemish coastal dunes, located between the cities of Nieuwpoort-Lombardsijde and De Panne [Belgium, 51°08'- 51°05'N, 2°45'- 2°32' E] and consisting of 149 discrete grey dune patches. Mean patch size is 1.41 ha and ranges from 0.07 –22.54 ha. Patch size and patch connectivity, as calculated for ballooning dispersal [see further], are significantly related [Bonte *et al.* 2003d], indicating that smaller patches are generally more strongly isolated.

All studied species [Table 1] are common in the Flemish coastal dunes, but specialised species may be rare at regional [Maelfait *et al*. 1998] or global level [Hänggi *et al*. 1995]. They represent more than 85% of the total number of individuals caught with pitfall traps [Table 1] and were the only collected in sufficiently numbers to perform tests on their aerial dispersal propensity [see below]. Spiders from grey dunes are generally small-sized and most active during autumn and spring [Bonte & Mertens 2003]. Stenotopic microsheet webspiders [Linyphiidae] are characterised by one generation in one year and have semi-sessile life habits, while larger species of crabspiders [Thomisidae] and wolfspiders [Lycosidae] have one generation yearly or bi-yearly [Bonte & Maelfait 1998; Bonte & Maelfait, unpub. data]. Most species live on the surface, or have a burying life style [*Arctosa* and *Alopecosa* species]. Voucher specimens are deposited at the Royal Belgian Institute of Natural Sciences in Brussels; nomenclature follows Platnick [2002].

Patch occupation and landscape characteristics

Presence-absence data of 29 spider species were derived from pitfall records in 19 grey dune patches. Each fragment was sampled during one year between 1995 and 2002 with five pitfall traps [the traps consist of uncovered glass jam jars with a diameter of 9.5 cm, filled with a 10% formaline soap-solution]. The traps were emptied fortnightly. All species included in the analysis are easily captured with pitfall traps because of their high degree of mobility and the short vegetation structure [Bonte *et al*., in press]. Pitfall data therefore reliably reflect species occurrence.

Patches were digitised from aerial orthophotographs with a Geographic Information System [Arcview 3.1] and discrimination of vegetation types was based on vegetation-specific red [RED] and near-infrared [NIR] reflectance values [Provoost *et al*. 2002]. Patch connectivity [*S*] was estimated as $S_i = \sum_{j \neq i} \exp[-\alpha d_{ij}] N_j$. [Hanski 1999b] with ? = constant describing the strength of the inverse relationship between numbers of migrants from patch j and distance between patches, d = the geographic distance between patch i and j, and N = population size at patch j. N was set as one for all patches, so S_i

reflects the optimal patch connectivity, irrespectively of the patch occupancy status. Based on literature data [Thomas 1996] we assigned a=4 for dispersal by ballooning [see below] independently of the surrounding matrix type. Values of patch size and patch connectivity were ln-transformed to approach normality. For this study, we selected grey dune patches in which patch size and connectivity were not significantly [r_{18}=0.289; NS] related.

Habitat specialisation

Species-specific levels of habitat specialisation were estimated from the level of maximal indicator value [IndVal] in a dichotomous and hierarchical clustering of pitfall data from different coastal dune habitats [details in Bonte *et al.* 2002a; Bonte *et al.* 2003d] as an approach of eurytopicity [Dufrêne & Legendre 1997]. This approach determines indicator species at different hierarchical or non-hierarchical levels of clustering by combining relative species abundance with its relative frequency of occurrence in the various groups of site within each level of clustering. Species with maximal IndVal at the last level [level 6] occur only in very specific habitats [grey dune], while those with a maximal IndVal at intermediate division levels are bound to more than one type of typical coastal dune habitat. Dispersing individuals accidentally trapped in a particular habitat only marginally influence the IndVal calculation due to the specific algorithm used [Dufrêne & Legendre 1997]. Additionally, because only data from three patches, included in this study, were used for this IndVal calculation, circular argumentation was avoided.

Aerial dispersal

Potential long-distance dispersal in *Araneae* species mainly occurs via passive transport in air currents, so-called ballooning dispersal [Weyman 1993], while short-distance dispersal is also possible by cursorial dispersal, especially in wolf spiders *Lycosidae* [Samu *et al.* 2003]. Ballooning dispersal is initiated by tiptoe behaviour, i.e. stretching of the legs and raising of the abdomen prior to silk thread production from the spinnerets [Duffey 1998]. Earlier studies confirmed that the frequency of tiptoe behaviour under laboratory conditions could be used as a reliable estimator of ballooning propensity in the field [Richter 1970, Weyman 1993, Bonte *et al*. 2003b,d]. To study tiptoe behaviour, spiders were either collected in the field [families Araneidae, Dictynidae, Linyphiidae, Gnaphosidae and Tetragnatidae] or reared from cocoons collected in the field [families Lycosidae and Thomisidae; protocol as described in Bonte *et al*. 2003d]. Only adult Linyphiidae and small juvenile spiders from the other genera were used for the experiment, since these have ideal masses for aerial dispersal [< 1mg: Greenstone *et al*. 1987]. Tiptoe behaviour was studied following Legel & Van Wingerden [1980] and Bonte *et al*. [2003d]. Spiders were placed on a plastic frame, individually or in groups of two to five individuals [in case of *Pardosa* juveniles reared in the lab] as to reduce the level of intraspecific interaction. The frame was placed in a windtunnel with an upward current of 1-1.2 m/s at a temperature of 30 ±2°C and an aerial humidity of 40-50%. To prevent spiders from escaping by walking, the frame was placed in water. Observations were conducted during 20 minutes. Observations of tiptoe behaviour of three seconds or more were considered valid [Bonte *et al*. 2003b]. Since nutritional conditions influence ballooning [Bonte *et al*. 2003b], spiders were fed with *Isotoma viridis* [Collembola] ad libidum before starving them for one week prior to the experiment.

Statistical analysis

Data on the occupancy of each species within each patch [binomial response; 0 or 1] were analysed with a mixed logistic regression model with logit link [glimmix procedure in SAS 8.1]. Variables 'tiptoe frequency', 'habitat specialisation', 'patch area', 'patch connectivity' and all relevant two-way interactions were modelled as continuous factors, with the degrees of freedom being approximated using Satterthwaite's procedure. Variable 'species' and the two-way interactions with variables 'patch area' and 'patch connectivity' were included as random factors and tested against the c? distribution [DF=1] of the Log-Likelihood-difference between the models with and without variable of interest. Non-significant variables were eliminated by a backward-stepwise procedure.

Table III.3-1 - Degree of habitat specialisation [data from Bonte et al. 2002a], frequency of tiptoe behaviour [data from Bonte et al. 2003d], the number of tested individuals n [with notes on the number of mothers in case of laboratory rearing], relative abundance within pitfall traps [total abundance = 8887 individuals] and percentage patches occupied by 29 Araneae species from coastal grey dunes [on 19 grey dune patches].

Species and family	**Habitat specialisation**	**tiptoe freq. [%]**	**n**	**Relative abundance [%]**	**Patch occupation [%]**
Alopecosa barbipes [Sundevall, 1833] [Lycosidae]	3	8.95	67 [6]	1.66	84.10
Alopecosa fabrilis [Clerck, 1757] [Lycosidae]	6	0.00	21	0.34	31.57
Alopecosa pulverulenta [Clerck, 1757] [Lycosidae]	2	16.36	55 [4]	1.67	100.00
Arctosa perita [Latreille, 1799] [Lycosidae]	2	20.90	110 [7]	0.72	78.94
Argenna subnigra [O.-P. Cambridge, 1861] [Dictynidae]	1	40.00	35	1.41	78.94
Centromerita concinna [Thorell, 1875] [Linyphiidae]	2	56.36	55	8.19	94.73
Erigone atra Blackwall, 1833 [Linyphiidae]	1	96.00	300	13.42	100.00
Erigone dentipalps [Wider, 1834] [Linyphiidae]	2	73.21	56	4.96	100.00
Hypsosinga albovittata [Westring, 1851] [Araneidae]	3	33.33	15	0.45	47.36
Meioneta rurestris [C.L. Koch, 1836] [Linyphiidae]	2	77.50	40	0.88	100.00
Ozyptila simplex [O.P.-Cambridge, 1862] [Thomisidae]	2	32.35	34	0.49	78.94
Pachygnatha degeeri Sundevall, 1830 [Tetragnathidae]	2	35.59	59	2.89	89.47
Parapelecopsis nemoralis [O.P.-Cambridge, 1884] [Linyphiidae]	2	10.56	123	0.92	68.42
Pardosa monticola [Clerck, 1757] [Lycosidae]	4	8.08	569 [22]	18.59	68.42
Pardosa nigriceps [Thorell, 1856] [Lycosidae]	1	42.26	97 [6]	1.97	100.00
Pardosa pullata [Clerck, 1757] [Lycosidae]	2	15.73	89 [7]	0.34	68.42
Pelecopsis parallella [Wider, 1834] [Linyphiidae]	5	20.58	34	4.01	63.15

Species and family	Habitat specialisation	tiptoe freq. [%]	n	Relative abundance [%]	Patch occupation [%]
Styloctetor romanus [O.P. Cambridge, 1872] [Linyphiidae]	6	12.68	134	0.38	78.94
Tenuiphantes tenuis [Blackwall, 1852] [Linyphiidae]	1	85.29	34	1.40	100.00
Thyphochrestus digitatus [O.P.-Cambridge, 1872] [Linyphiidae]	5	10.95	210	6.43	73.68
Tiso vagans [Blackwall, 1834] [Linyphiidae]	3	46.87	32	0.60	78.94
Trichopterna cito [O.P.-Cambridge, 1872] [Linyphiidae]	3	22.98	87	3.42	73.68
Walckenaeria monoceros [Wider, 1834] [Linyphiidae]	2	45.83	48	0.60	73.68
Walckenaeria stylifrons [O.P.-Cambridge, 1875] [Linyphiidae]	6	4.34	23	0.51	57.89
Walckenanaeria antica [Wider, 1834] [Linyphiidae]	1	88.23	34	0.19	94.73
Xysticus kochi Thorell 1872 [Thomisidae]	3	32.30	65 [3]	4.31	94.73
Xysticus ninnii [Thorell, 1872] [Thomisidae]	5	0.00	21 [1]	0.19	15.78
Xysticus sabulosus [Hahn, 1832] [Thomisidae]	4	13.63	110 [6]	0.97	57.89
Zelotes electus [C.L. Koch, 1839] [Gnaphosidae]	2	36.00	25	3.52	100.00

Results

Data on patch occupancy, ballooning frequency and degree of habitat specialisation are summarized in Table III.3-1.

The probability of patch occupancy was positively related to the frequency of tiptoe behaviour. The regression slope was estimated to 2.868 ± 2.598, back-transformed equalling 0.935 [range 0.515-0.995] [Table 2; Fig. 1]. The effect of patch connectivity depended on patch area, as shown by a significant area*connectivity interaction [Table 2]. When both area and connectivity increased, fragments were more likely to be occupied. However, connectivity did not affect patch occupancy when patches were small [Fig. 2]. Patch occupancy varied significantly between species [σ^2=0.408], with the effect of species depending on the degree of connectivity [species*connectivity: σ^2=0.013] [Table 2]. The residual variance equalled 0.764. The goodness-of-fit of the models was significant [σ^2_{527}=359.11, p<0.0001].

Table III.3-2 - Logistic regression model analysing the effects of tiptoe frequency [TTfreq], degree of habitat specialisation [IndVal], patch area [Area] and patch connectivity [S] on patch occupancy by 29 Araneae species from coastal grey dunes.

Variable	**num. d.f.**	**den. d.f.**	*F*	*p*
TTfreq	1	40.9	24.56	<0.001
IndVal	1	302	0.30	0.584
Area	1	519	1.31	0.254
S	1	517	8.56	0.004
TTfreq x IndVal	1	20.1	0.06	0.815
Area x S	1	519	6.20	0.013
Area x TTfreq	1	50 1.	18	0.282
Area x IndVal	1	43	0.25	0.624
S x IndVal	1	241	0.62	0.432
S x TTfreq	1	410	0.73	0.392
Variable		σ^2	χ^2_1	*p*
Species		0.408	98.2	<0.0001
Species x S		0.013	10.7	0.0005
Species x Area		<0.001	0.114	0.735
Species x Area x S		<0.001	0.008	0.928

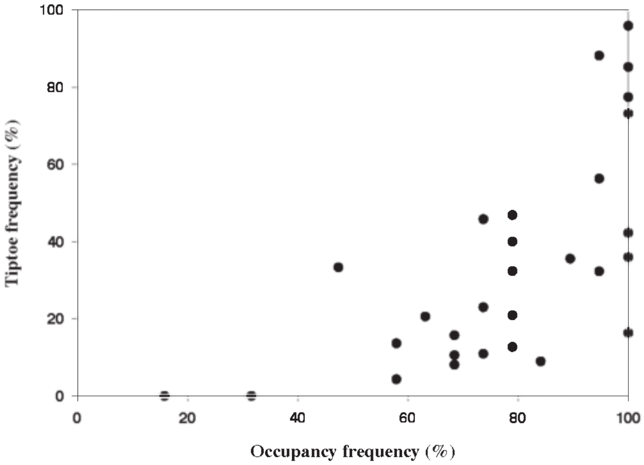

Fig. III.3-1: Relationship between frequency of tiptoe behaviour and the number of occupied patches by 29 spider species of fragmented grey dunes.

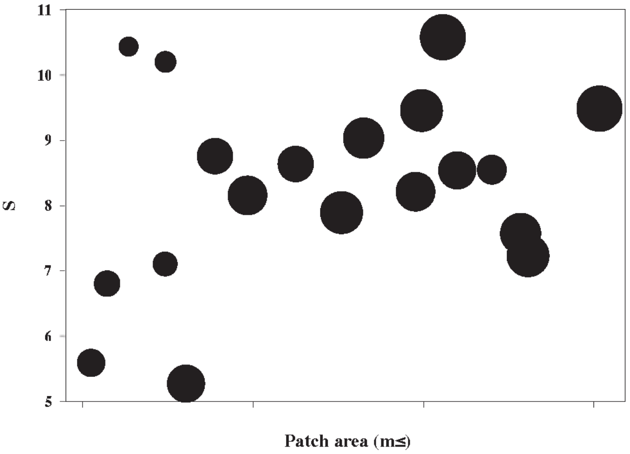

Fig. III.3-2: Number of species per patch for 29 spider species in relation to landscape levels of patch connectivity and patch size. Sizes of the dots reflect the proportion of present species on the total number of studied species.

Discussion

The distribution of spider species depends on their aerial dispersal potential, and the interaction between patch connectivity and area. Niche breadth, measured as the degree of habitat did not contribute to the observed distribution patterns. Residual variation was explained by species-specific responses to the degree of patch connectivity for ballooning dispersal.

Ballooning is presumed to be an efficient mechanism for distant dispersal and hence for colonisation of suitable but unoccupied habitats [Toft 1995; Duffey 1998]. In severely fragmented landscapes, suitable habitats are patchily distributed within an unsuitable matrix. Especially for species with strict and specialised habitat requirements, aerial dispersal may involve a high risk in reaching potentially suitable habitats. This was confirmed in an earlier study on dispersal by spiders in grey dunes where selection against ballooning dispersal in specialist species was believed to result from local adaptation [Bonte *et al.* 2003c]. Effective wind dispersal has been strongly linked to colonisation ability in a number of plant species [*e.g.* Dwzonko & Loster 1992; Nakashizuka *et al.* 1993; Stöcklin & Bäumler 1996], while ballooning in spiders has also been shown to be effective in the colonisation of recently cleared land [Meijer 1977, Weyman & Jepson 1994]. A recent study of a spatially-structured population of wolf spiders [Bonte *et al.* 2003c], however, failed to confirm the importance of ballooning in short-term colonisation, although it was the best predictor for patterns of patch occupancy resulting from long-term colonisation and extinction dynamics. Results from this study generalise this conclusion that long-term patch occupancy patterns are related to ballooning dispersal for the entire spider assemblages of grey dunes.

This study, however, does not show a relationship between level of habitat specialisation and species distribution, which would be expected if specialist spiders were more sensitive to changes in habitat quality. It does neither explain patterns in species distribution in interaction with connectivity, which would indicate different sensitivities to patch isolation for specialist and generalist species. Such a relationship would be expected if generalist species survived better in other habitat types in the shrub matrix. When a different index of niche breadth was used [negative logarithm of the number of suitable habitats of the species in Central-Europe; details in Bonte *et al.* 2003c], comparable results were obtained [data not shown], confirming the validity of our conclusions. Because niche breadth and ballooning propensity are positively related [Bonte *et al.* 2003c], low occurrence of specialised species in small and isolated grey dune fragments [Bonte *et al.* 2002a] seems largely due to their low ballooning ability. As a result, specialised [hence intrinsically rare] species can be predicted to become rarer if fragmentation increases and connectivity decreases.

Since we used the degree of habitat specialisation in coastal dunes as a measure of niche breadth, effects of realised niches rather than of Hutchinson's fundamental niches were analysed. As pointed out by Pulliam [2000], species can survive outside their fundamental niche, although local mortality may exceed recruitment in case of a source-sink population structure. We recorded the presence of species for which the presumed optimal habitat is productive [often arable] grasslands [*Erigone atra, E. dentipalpis, Meioneta rurestris, Tenuiphantes tenuis*; Hänggi *et al.* 1995]. Because prey abundance tends to decrease during summer [Bonte & Mertens 2003], summer mortality can be expected to be very high for these grassland species. Their presence in grey dunes was therefore probably mediated through continuous aerial colonisation from neighbouring source habitat [i.e. dune slacks, wet meadows]. In contrast, specialist species for which the fundamental niche consists of grey dunes [*Alopecosa fabrilis, Styloctetor romanus, Walckenaeria stylifrons*] can be expected to be absent due to limited dispersal ability. Results from our study therefore suggest that dispersal ability largely affects our perception of a species 'fundamental niche' [Pulliam 2000], and that source-sink and metapopulation dynamics may have a major impact on the distribution of species. If effects of fundamental niche breadth [e.g. through study of desiccation resistance and/or temperature optima; Almquist 1970; Almquist 1971] rather than realised niche breadth could be analysed, model outcomes might differ in the direction expected. Yet, in a study on regional and national distribution patterns of herb species [Thompson *et al.* 1999] the degree of habitat specialisation [realized niche] rather than germination temperature [fundamental niche] explained the largest variation species range.

Apart from species-specific traits, landscape characteristics significantly explained variation in patch occupancy. Regression coefficients describing the relationship between patch occupancy and patch connectivity, varied between –2.12 and 2.13 [29 species tested; after Bonferroni correction none of the regressions were significant]. Such variation was likely due to the presence of other dispersal modes, i.e. cursorial dispersal, which may be more efficient in larger species as demonstrated by Bonte *et al.* [2003c] for the wolf spider *Pardosa monticola*. Besides, individual- and population-level factors such as longevity, population size, population density, and sensitivity to low densities [Allee effect; Stephens & Sutherland 1999] may affect extinction probability and hence distribution patterns.

In conclusion, we have given evidence that aerial, passive dispersal shapes species distribution. The inclusion of data on niche breadth, although here not contributing to the overall model, may elucidate species distributions, apparently not influenced by dispersal characteristics [Andersson et al. 2000; Malmqvist 2000; Clarcke et al. 2001]. From a conservationist point-of-view, our results show that fragmentation will accelerate the extinction of specialised species if fragmentation rates of their habitat keep on increasing.

Acknowledgement

We would like to thank P. Criel and T. Buysse for identifying spiders from grey dune patches in the dune areas ‘De Westhoek - De Panne’ and ‘Les dunes fossils - Ghyvelde’ within the framework of their master-thesis. We are also grateful to the Nature division of the Flemish community [ir. J.-L. Herrier] for the permission to sample some fragments and partly financing this study within the framework of the monitoring of the nature management.

III.4 ENVIRONMENTAL AND GENETIC BACKGROUND OF TIPTOE-INITIATING BEHAVIOUR IN THE DWARFSPIDER *ERIGONE ATRA*


FOTO: STEVE HOPKIN

BONTE D., DEBLAUWE I. & MAELFAIT J.-P. 2003. *Animal Behaviour* 66: 169-174

Abstract

Ballooning is a widespread behavioural trait in invertebrates, which enhances passive aerial dispersal. We investigated the influence of common lineage [family effect] and postnatal environmental conditions on latency to initiate preballooning tiptoe behaviour [ballooning latency] in the dwarfspider Erigone atra *[Blackwall, 1841]. Spiders were individually tested in a specially designed test chamber for the latency to perform ballooning initiating tiptoe behaviour. In a 3-week experiment, in which the spiders were fed only during the first day of each week, ballooning latency had low repeatability at week intervals. Ballooning latency declined with increasing food deprivation during the first week but not during the second and the third weeks. At intervals of less than 1 h however, ballooning latency showed high repeatability. We also investigated whether maternal and postnatal environmental conditions [i.e. during juvenile development] influence phenotypic variation in ballooning latency. We reared offspring of several families under two feeding and two temperature conditions. Environmental conditions explained more variation in ballooning latency than family. Ballooning latency was lower in spiders reared at 20°C than in those reared at 15°C. In addition, spiderlings fed four prey per 3 days were faster ballooners than those fed only four prey per week. An interaction between factors was present, indicating the existence of different reaction norms between the two environmental conditions. The expression of ballooning latency behaviour thus strongly depends on current nutrition, feeding history and the feeding and temperature conditions during juvenile development.*

Keywords: Araneae, ballooning, dispersal, juvenile development, GxE interaction

Introduction

Aerial dispersal is common among terrestrial insects and spiders. In the latter, this mode of dispersal is known as ballooning. The spider climbs to an elevated starting point, stretches its legs and raises its abdomen [tiptoe behaviour]; it then produces long silk threads and is finally carried up by the air current [Jones 1996a,b]. Aerial dispersal is effective for both distant migration [possibly affecting gene flow] and for local dispersal [Thomas 1996], especially in ephemeral but highly productive habitats where rapid movement under unfavourable conditions is important for survival [Legel & Van Wingerden 1980; Van Wingerden 1980; Morse 1993; Duffey 1998]. Tiptoe behaviour is typical of aerial dispersal in spiders of the Linyphiidae and juvenile Lycosidae and can be easily observed under laboratory conditions [Weyman 1993]. *Erigone atra*, one of the commonest spiders of open habitats in the temperate regions of the northern hemisphere, has a strongly developed ballooning behaviour. This species is often one of the first pioneers on regularly disturbed, especially agricultural, land [De Keer & Maelfait 1988 a,b].

Ballooning in spiders has mainly been studied in field conditions, especially within the framework of timing of dispersal [Dean & Sterling 1985; Greenstone *et al*. 1987; Blandenier & Fürst 1998; Bonte *et al*. 1998] and in relation to spider densities and activities in the field [Greenstone *et al*. 1985b; Weyman *et al*. 1995]. Laboratory studies have largely focused on the relation between aeronautic behaviour and meteorological conditions such as wind velocity and temperature [Van Wingerden & Vugts 1974; Vugts & Van Wingerden 1976; Greenstone 1990], and on the importance of crowding and food shortage as a trigger for this behaviour [Legel & Van Wingerden 1980]. Ballooning is triggered by acute food shortage [Weyman *et al*. 1994], low wind velocities [<3 m/s] and a high temperature inversion during the morning [Richter 1970; Van Wingerden & Vugts 1974; Vugts & Van Wingerden 1976; Greenstone 1990; Duffey 1998], and its frequency differs between species [Richter 1970; Van Wingerden 1980; Greenstone 1982; Miller 1984]. Differences between populations, however, have not been unambiguously demonstrated [Richter 1971].

Little experimental work has been carried out on factors underlying the initiation of ballooning behaviour, or on genetic variance underlying phenotypic variation [Weyman 1993]. Several studies have shown that wing dimorphism is under polygenic control [Järvinen & Vepsäläinen 1976; Roff 1986; Kaitala 1988; Desender 1989a] and Li & Margolies [1993] found additive genetic variation for dispersal behaviour in the two-spotted spider mite, *Tetranychus urticae*. In the latter study, however, nonadditive genetic variation and maternal effects or common environmental variation explained the largest part of the phenotypic variation, and covariation with fecundity and sex ratio was found. A major problem exists in estimating heritability of behavioural traits because of their low level of repeatability caused by difficulties in keeping experimental conditions or the individual's internal state constant [Kecic & Marinkov 1974].

We investigated [1] the repeatability of preballooning behaviour [2] the extent to which variation is determined by environmental circumstances during juvenile development, and [3] the extent to which a family effect is present. Such factors could possibly contribute to similarity in offspring dispersal behaviour, as demonstrated by Massot & Clobert [2000]. Family effects include maternal effects and possible additive heritabilities. Postnatal effects include common environmental conditions and [social] interactions between siblings. Relations between offspring dispersal and maternal and offspring characteristics can result from both genetic and environmental factors [Kirkpatrick & Lande 1989] and are very informative about the nature of dispersal. Our aim was therefore to investigate whether family effects or postnatal environmental conditions influence preballooning behaviour [i.e. the latency to show tiptoe behaviour].

Although behaviours such as climbing vegetation and taking off are also important factors in aerial dispersal [Weyman 1993], studies on the latency to initiate tiptoe behaviour are needed to understand variation in the spider's motivation to disperse by ballooning under suitable meteorological conditions. Fast-reacting individuals under laboratory conditions are more likely to balloon under variable weather [wind velocity] conditions and under sudden unsuitable environmental conditions in which spiders have to escape from their original habitat.

Methods

General Methods

We tested the propensity to express tiptoe behaviour under constant climatological conditions, using a test chamber based on the recommendations of Legel & Van Wingerden [1980]. Spiders were placed on a plastic frame in an air tunnel with upward currents at a temperature of 30 ± 2°C, aerial humidity of 40-50% and a light breeze, velocity 1-1.2 m/s. To prevent the spiders from escaping, we placed the frame in a bath of water. Because all individuals expressed the tiptoe behaviour within 10 min., we measured the latency [to the nearest second] of the spider to initiate this behaviour [ballooning latency] from the onset of wind turbulence. To be valid, a minimum of 3 s of constant tiptoe behaviour needed to be observed.
With the exception of the 3-week repeatability experiment [see below], all individuals were tested 1 day after moulting to the adult stage, to minimize variation in internal state. Spiders were not acclimatized to the climate conditions in the test chamber.

We collected gravid female spiders randomly at the end of September 1999 in grass tussocks in a pasture of the Westhoek dune reserve in De Panne [Belgium]. Because the species is abundant throughout the year, individuals strictly dependent of ballooning for temporal site colonisation were not selected. The adult instars of their offspring were used for laboratory experiments. Spiderlings were reared in petri dishes [diameter 5 cm] on plaster of Paris under a relative humidity close to saturation and a light:dark cycle of 16:8 h . The collembolan *Isotoma viridis* was used as prey. Because we wanted to investigate how different environmental conditions influence ballooning behaviour, we imposed four different rearing treatments by combining two temperature regimes [low:15°C ; high:20°C] and two diet regimes [well fed: four prey/3 days; poorly fed: four prey/week]. All prey offered were consumed, and mortality was low [5.2 %].

Latency data were ln transformed and did not differ from a normal distribution [Kolmogorov Smirnov test: NS].

Repeatability and Acute Stress

To measure repeatability over short intervals, we tested 38 randomly selected individuals twice within 1 h. Individual ballooning latencies were compared by intraclass correlation coefficients [t], calculated from a one-way ANOVA with individual as factor [Lessels & Boag 1987; Boake 1989; Sokal & Rohlf 1995]. An intraclass correlation coefficient close to 1 indicates a high repeatability, one close to zero none. We examined the repeatability at longer intervals, that is, with variable periods of food stress, in 20 spiders kept at 20°C during a 3-week experiment, in which they were fed only on the first day of each week. Consequently, they experienced increasing food deprivation effects for the rest of the week. Ballooning latency was tested each day. Intraclass correlation coefficients for ballooning latency were calculated between days when spiders were assumed to be in the same nutritional state [day after spiders were fed, 1-week intervals]. All analyses were performed with SAS 8.1; variation due to the random individual effect [intraclass correlation] was tested against a model including all variance components [χ^2_1-test of difference in log-likelihood]. Statistical tests were two-tailed.

Developmental conditions and Family

We randomly assigned spiderlings from 13 females to the four rearing conditions described above, and tested them 1 day after final moult under well-fed conditions. Preliminary experiments indicated that gender did not influence ballooning latency [unpublished data]. We applied a General Linear Model with type III sum of squares, family [genotype] as a random factor and temperature and feeding conditions as fixed factors. In this way, our data were analysed in a quantitative genetic framework with genotype x environment interaction, whereby genotype included nonadditive components, prenatal maternal and paternal effects. We used 284 individual spiders from 13 families [mean 5.04 siblings/treatment]. Variance estimates, contributed by special environmental effects [as a consequence of random developmental noise and microenvironmental variation], genotype and genotype x environment interactions were calculated from the expected mean squares under a mixed model [Lynch & Walsh 1998]. Because of the specific mean squares configuration, fixed [macroenvironmental] factors did not explain any of the variation [Lynch & Walsh, 1998].

Relations with Life History Traits

We measured development time to maturity [to the nearest day] and size of the spider [cephalothorax size in mm^2 digitized under a 50x binocular microscope] for the offspring of 24 females reared with prey ad libitum at 20°C. These data were used for the analysis of possible correlations with the ballooning latency. In addition, we measured female size [measured in the same way as for the offspring] and the number of offspring in the first cocoon [fecundity as maternal fitness characteristic]. The sex ratio in the first cocoon was also determined. Because fecundity was correlated with the size of the female [Pearson correlation: $r148=0.268$, $P<0.05$], we used residuals of the regression of number of eggs in the first cocoon on female size as a fitness measure.

Results

Repeatability and Acute Stress

Ballooning latency did not differ significantly between the two tests conducted within 1 h and where highly repeatable [mean values ± SD; test 1: 110.66 ± 66.90; test 2= 87.94 ± 50.91; $t = 0.781$; random effect: $\chi^2_1 = 43.5$; $P<0.001$]. At 1-week intervals it decreased and was less repeatable [range: 0.306-0.708]. Ballooning latency decreased significantly over the first week of the 3-week experiment [Pearson correlation: $r18 = 0.270$, $P<0.05$] but not during the second [Pearson correlation: $r18 = 0.014$, NS] and the third weeks [Pearson correlation: $r18 = 0.0008$, NS] [Fig. III.4-1].

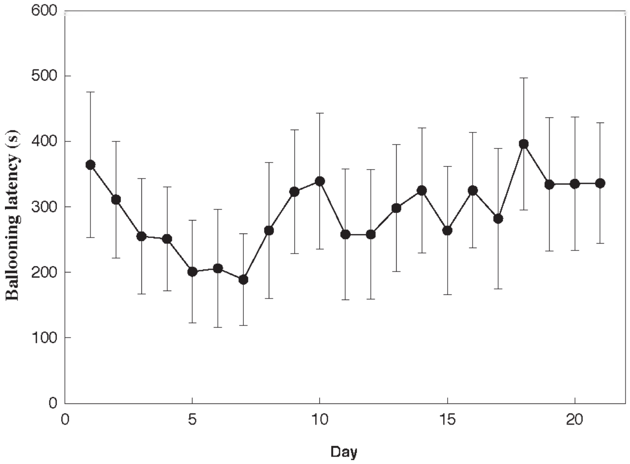

Fig. III.4-1: Ballooning latency [mean ± 95% confidence intervals, s] over a 3-week experiment in which 20 spiders were fed only on the first day of the week [arrow].

Developmental Conditions and Family

Phenotypic variation in ballooning latency could be attributed to feeding and temperature conditions during juvenile development, but not to genotypic [family] effects [Table III.4-1]. Levels of ballooning latency were significantly higher at 15°C than at 20°C and higher with the poor diet [Fig. III.4-2]. Mean latency did differ significantly between temperatures [mean values ± SE: 15°C: 4.979 ± 0.783; 20°C: 5.493 ± 0.541, post hoc Scheffé $P<0.001$] but not between diet treatments [mean values ± SE: poorly fed: 5.251 ± 0.625; well fed: 5.320 ± 0.674, post hoc Scheffé, NS]. The interaction between temperature and diet was, however, significant: when poorly fed, spiderlings reared at 20°C increased ballooning latencies, and those reared at 15°C decreased it.

Genetic variation explained 29.2% of the total phenotypic variation [partitioned as 16.0% for genotype and 13.2% for all genotype x environment interactions]; the remaining variation could be attributed to microenvironmental variation [70.8%; Table III.4-1].

Table III.4-1 - Results of the GLM for ballooning latency [ln transformed] on the factors temperature, diet [both fixed] and family [random]. NE: No estimates available.

Factor	Sum of squares	df	Mean square	*F*	*P*	Variance estimates
Temperature	8,456	1	8,456	8,222	0.012	NE
Diet	1,927	1	1,927	5,159	0.036	NE
Family	30,948	12	2,579	3,720	0.159	0.105
Temperature x Diet	3,201	1	3,201	4,327	0.032	NE
Temperature x Family	13,413	12	1,117	1,426	0.273	0.065
Diet x Family	4,308	12	0.359	0.458	0.904	-0.010
Temperature x Diet x Family	9,402	12	0.784	1,648	0.070	0.032
Error	121,424	261	0.465			0.465

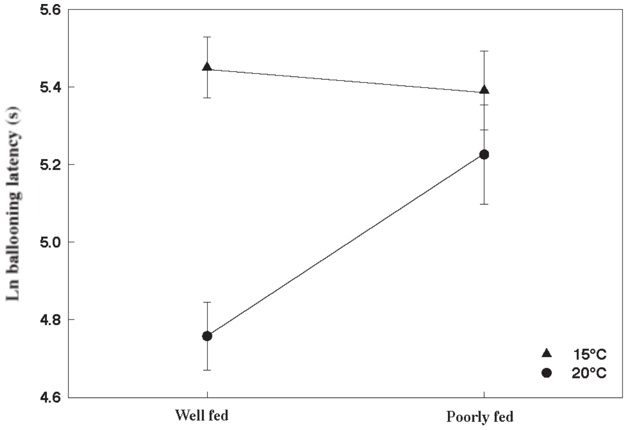

Fig. III.4-2: Ballooning latency [mean ± SE, s] of spiders that, as juveniles, were reared at 15 or 20°C and were either well fed or poorly fed [four prey per 3 or 7 days].

Relations with Life History Traits

For males and females separately, no relation between ballooning latency and size at maturity was found [males were significantly larger than females: t test: t236=10.45, P<0.001; Table III.4-2]. Development time to maturity was independent of sex [t278= 0.116, NS] and did not show a significant correlation with ballooning latency for the well-fed individuals reared at 20°C [Table III.4-2]. If we include all observations from the four-environments experiment, a significant positive correlation was found with development time increasing in the order high temperature/well fed, high

Table III.4-2 - Life history traits of offspring and their mother, and correlations between traits and ballooning latency. *Pearson correlations for offspring traits and Spearman rank correlations for mother's traits

			correlation	
Life-history trait	**Mean value ± SD**	N	r^2	P
Offspring				
Development time [days]				
All conditions	39.23 ± 5.18	280	0.220	<0.001
At 20°C, spiders well fed	22.05 ± 3.34	248	0.067	NS
Cephalothorax size at maturity [mm^2]				
Males	3.34 ± 0.21	117	0.142	NS
Females	3.09 ± 0.16	125	0.042	NS
Mother				
Offspring sex-ratio [males/females] 0.87	± 0.38 24	-0.129	NS	
Adult cephalothorax size [mm^2]	3.20 ± 0.03	24	-0.259	ns
Number of offspring in first cocoon	14.00 ± 3.95	24	0.146	ns
Residuals of offspring on mother's size	-	24	-0.306	ns

temperature/poorly fed, low temperature/well fed and low temperature/poorly fed. Both temperature and diet contributed to this difference [ANOVA: temperature effect: F1,280 = 354.921, P<0.001; diet effect: F1,280=33.927, P<0.001]. No significant relations with maternal life history traits were found [Table III.4-2].

Discussion

Our laboratory experiments showed high repeatability of latency to express preballooning behaviour under stress [when the spider had to escape from the test chamber to survive at a relatively high temperature] at short intervals of 1 h, but low repeatability at longer intervals of a week. Phenotypic variation was determined mainly by environmental conditions and less so by genotypic effects. Relations with individual and maternal fitness characteristics were not found.

Our results confirm that tiptoe behaviour in erigonid spiders is strongly influenced by food deprivation [Van Wingerden & Vughts 1974; Legel & Van Wingerden 1980; Weyman & Jepson 1994; Weyman et al. 1994]. This pattern was found only during the first week of food deprivation, however, and not during food deprivation in the next 2 weeks. This result indicates that ballooning latency depends not only on acute feeding stress but also on feeding history and age. Because of this low repeatability, it is difficult to make representative multiple measurements and to estimate the trait heritability under different environmental and internal conditions. The lack of multiple measurements has led to underestimation of the levels of heritability of courtship and mating speed in Drosophila [Hoffmann 1999]. The male-biased sex ratio during ballooning in the field [Blandenier & Fürst 1998; Bonte et al. 1998] cannot be attributed to a different tiptoe-initiating behaviour, because the latter was independent of sex.

Different environmental conditions during juvenile development markedly affected the latency to initiate preballooning behaviour. Both the feeding regime and the temperature had a significant effect. The effect of temperature was clear: spiders reared at 20°C took off faster than those reared at 15°C. The finding that the juvenile diet influenced the adult's ballooning latency was as predicted; however, our results showed an effect of temperature as well. Ballooning latency was shorter for spiders that were well fed during development when the temperature was high [20°C], but at the lower breeding temperature, there was only a marginal significant difference between diets. An interaction between diet and temperature was thus present, indicating a complex reaction of spiders to different postnatal environmental factors.

The strong effect of temperature during rearing on ballooning latency may be an inherent physiological response. Flight activity in Oncopeltus also changes significantly with temperature during development [Dingle 1968], suggesting a physiological depression near temperatures at the threshold where reproduction is possible. In the carabid beetle Pogonus chalceus, where dispersal potential is related to wing size, temperature during development did not alter the relative wing length [Desender 1989a]. High temperatures over the summer could thus act as an extra trigger for the stimulation of the mass late-summer ballooning, commonly observed in this species [Bonte et al. 1998; Duffey 1998], although an interaction with temperature during ballooning is to be expected. Nevertheless, our data indicate that ballooning latency is influenced by physiological responses to environmental circumstances during juvenile development. Mothers are thus able to influence the ballooning initiation of their offspring by the choice of habitat for reproduction.

Different nutritional conditions during juvenile development induced different behavioural ballooning patterns, in contrast to acute food stress, which is the final trigger for ballooning in many spiders [Van Wingerden & Vughts 1974; Legel & Van Wingerden 1980; Weyman & Jepson 1994; Weyman et al. 1994; Bonte & Maelfait 2001]. Our findings contradict those of Legel & Van Wingerden [1980], who found a lower percentage of ballooners in tested spiders when individuals were reared under well-fed and medium-starved regimes [40 and 37.5 %] than with greater levels of starvation. Their model organism was *Erigone arctica* [White, 1852], a sister species typical of salt marshes. Although the power of their experiment was too low for appropriate statistics, their results indicate again that feeding conditions during development alter ballooning capacity. Different species can apparently react in different ways to changing environmental conditions. Since the temperature during rearing in their experiment was rather high [room temperature between 18 and 23 °C], similar results to ours could be expected.

Our results suggest that ballooning latencies in E. atra are short only in high productive habitats, where preys are abundant and temperatures high. As we observed covariance between development time in the four treatments and ballooning latency, variation we observed in ballooning latency can be explained by variation in development time. In our experiment, however, ballooning latency is not correlated to development time within the separate rearing conditions and is consequently probably not the main trigger responsible for the observed variation in ballooning latency under laboratory conditions.

Family effects explained about 16% of the observed phenotypic variation. Although not statistically significant [only 13 families were included in the quantitative study], this genotypic source of variation was not negligible. It stresses the importance and interaction of genetic components in the expression of behavioural traits, narrowly linked to dispersal. This biologically relevant, low genotypic source of variation is concordant with Roff &

Mousseau's [1987] and Hoffmann's [1999] findings of overall low heritabilities for behavioural traits. We did not find any relation between offspring ballooning latency and maternal fitness characteristics. The probability of ballooning by young crab spiders Misumena vatia also did not differ with clutch size or individual size [Morse 1993]. Morse [1993] also found an effect of substrate, which was related to immediate prey availability. Consequently, the choice of nest sites [substrate] by the spiderlings' mothers indirectly affected the spiderlings' dispersal behaviour. Our results are thus in agreement with Morse's [1993] findings that variation in spider ballooning is only marginally determined by evolutionary components. More empirical research is needed to understand the possible sources of variation in ballooning behaviour.

In insects with distinct dispersal characteristics such as wing polymorphisms and differentiated muscle development, maternal and additive genetic effects influence the total phenotypic variation [e.g. Janssen et al. 1988; Leamy 1988; Desender 1989a]. In full and half sibling, direct and indirect selection experiments; Li & Margolies [1993, 1994] found a relatively high heritability of ballooning latency in the arachnid [phytophagic] mite Tetranychus urticae. Li & Margolies minimized the residual variance during the experiments to 43-60%; and they estimated the additive genetic component to be 22.39%. Because of the strong influence of environmental factors and the impossibility of conducting multiple measurements, analogous experiments on ballooning behaviour in spiders are probably difficult to conduct in a standardized way.

In summary, we conclude that, in addition to [extensively documented] acute starvation, environmental variation during juvenile development influences ballooning latency in *E. atra* under our laboratory conditions. The habitat choice of the mother is therefore likely to influence offspring ballooning behaviour. A low, but biologically relevant, genotypic source of variation was, however, detected indicating that environment and genotype sum and interact in the expression of this dispersal-linked behavioural trait.

Acknowledgement

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III.5 PATCH QUALITY AND CONNECTIVITY INFLUENCE SPATIAL DYNAMICS IN A DUNE WOLFSPIDER

FOTO: JOHAN DE MEESTER

BONTE D., LENS L., MAELFAIT J.-P., HOFFMANN M. & KUIJKEN E. 2003. *Oecologia* 135: 227-233

Abstract

The spatial population dynamics of the wolfspider Pardosa monticola, *inhabiting patchily distributed grasslands in the Flemish coastal dunes from Belgium and Northern France were investigated with incidence function models using field survey data from 1998 and 2000. Vegetation height and patch size were related to habitat quality. Mark-recapture experiments revealed maximum cursorial dispersal distances of 280 m for moss dunes and 185 m for higher dune grassland. Higher shrub vegetation appeared to be dispersal barriers. These habitat-dependant cursorial distances and the theoretically estimated ballooning distance were included with patch distances into a connectivity index for both dispersal modes. Forward multiple regression indicated that patch occurrence was influenced by habitat quality and ballooning connectivity. Habitat quality and cursorial connectivity explained patterns in short-term colonisation. Extinction appeared to be stochastic and not related to habitat quality and connectivity.*

Genetic differentiation and variability was low. The discrepancy between the estimated low dispersal capacity and the indirect estimate of gene flow F_{ST} *indicates that historical population dynamics and/or historical ballooning dispersal influence the genetic structure in this species.*

Keywords: ballooning, cursorial dispersal, incidence function model, metapopulation, population genetics

Introduction

The presence of species in patchy landscapes can either be characterised by a patchy population structure [Hanski 1999a] or a metapopulation structure [Harrison 1991; Hanski 1999a]. In the first system, individuals move freely among habitat patches, while in the second, most individuals stay in a single patch during their entire life, but dispersing individuals enhance strong colonisation-extinction dynamics. This results in a population structure in which suitable patches remain vacant. Besides the colonisation abilities, changes in habitat quality also attributes to local extinction dynamics, as demonstrated for specialised butterflies [*e.g.* Thomas *et al.* 1992; Ravenscroft 1994; Moilanen & Hanski 1998; Bergman 1999] and backswimmers of the genus *Notonecta* [Briers & Warren 2000]. Patch-specific emigration and immigration rates can thus depend on patch area, intrinsic quality, geographic isolation and connectivity. These parameters together result in "mixed" population structures, with high migration rates for close, connected patches, and low rates for more isolated ones [Sutcliffe *et al.* 1997]. Such turnover- and migration dynamics alter the genetic structure of the inhabiting populations [Leberg 1992; Hasting & Harrison 1994]. In strongly connected populations, genetic differentiation will be low due to substantial gene flow, while strongly isolated populations can be expected to be highly differentiated. Turnover events in poorly connected populations may also negatively affect their level of genetic variability. Low gene diversity can further decrease population viability due to inbreeding effects leading to low individual fitness [Britten 1996; David 1998].

As the study of metapopulation dynamics requires knowledge on dispersal ability, empirical research has mainly concentrated on larger invertebrates which allow easy marking and tracking [*e.g.* butterflies: Harrison *et al.* 1988, Thomas & Harrison 1992, Thomas *et al.* 1992; grasshoppers: Hjerman & Ims 1996, Appelt & Poethke 1997, Kuhn & Kleyer 2000]. Few studies have dealt with dispersal of spiders, except for some larger Pisauridae species [Kreiter & Wise 2001]. Spiders can disperse in two distinct ways: either by cursorial movement [mainly adults] or by aerial ballooning [restricted to juveniles for the larger species]. Both modes of dispersal differ in their level of efficiency. Cursorial dispersal allows short distant movements only and its efficiency depends on the structure of the habitat matrix through which dispersal occurs [Bonte & Maelfait 2001]. Aerial dispersal, in contrast, is more efficient for long distant movements but involves a great risk of arriving in an unsuitable habitat. The study of ballooning efficiency has mainly been based on field observations and has been generalised with mathematical models [Thomas 1996]. Indirect estimates of dispersal, estimated by population genetic analyses, are more common [Boulton *et al.* 1998; Ramirez & Fandino 1996; Ramirez & Haakonsen 1999; Gurdebeke *et al.* 2000].

This paper reports on the metapopulation dynamics of *Pardosa monticola*, a wolf spider inhabiting short dune grasslands along the Flemish coast. Due to increased urbanisation for tourist facilities, the total area of dune habitat decreased from 6000 ha to less than 3800 ha since the beginning of the 20th century, and became increasingly fragmented [Vermeersch 1986]. After the Second World War, local farmers abandoned their agropastoral activities, which resulted in an overall increase of Sea Buckthorn-shrubs [*Hippophae rhamnoides*]. This, in combination with a crash of the rabbit [*Oryctolagus cuniculus*] population due to viral diseases myxomatosis and VHS, lead to a strong reduction and fragmentation of *Polygalo-Koelerion* grasslands [Provoost & Van Landuyt 2001].

Because of its larger size and typical habitat, the presence of *Pardosa monticola* in grassland fragments can be easily recorded, especially during sunny days, when both males and females are very active. This allowed us to conduct an experiment for the estimation of spider cursorial dispersal. Estimates of female cursorial dispersal and ballooning, the biological most relevant measures for patch colonisation and population establishment in the study species, were then used in an incidence model [Hanski 1994; Hanski 1997]. This model requires a limited number of parameters to be estimated, and makes biologically sound assumptions: dispersal is assumed to be distance dependent and colonisation and extinction processes are assumed to depend both on patch quality and patch connectivity [Moilanen & Hanski 1998]. To compare direct estimates of actual dispersal with indirect estimates of gene flow, we also conducted a population genetic analysis based on allozyme electrophoresis.

Material and methods

Study species and area

The wolfspider, *Pardosa monticola*, a widespread species in Europe and Asia, typically occurs in short and oligotrophic pastures and heathlands [Wiebes & Den Hollander 1974; Alderweireldt & Maelfait 1990]. In Flemish and Dutch coastal dunes, the species prefers mesophytic pastures grazed by rabbits and young dune slacks with a moderate vegetation coverage, where it is known to survive periods of flooding during winter [Van der Aart 1975; Maelfait *et al.* 1989; Bonte & Maelfait 2001]. Due to its regional scarcity, the species is listed on the Flemish Red List of endangered spiders [Maelfait *et al.* 1998]. During winter, *P. monticola* retreats in rough, litter-rich vegetation. Especially males show diffuse cursorial dispersal on grey dunes with different amounts of bare sand [Bonte & Maelfait 2001]. Ballooning by spiderlings has preliminary been studied under laboratory conditions where it has been observed after starvation and in a small proportion [6-10 %] of the population only [Bonte & Maelfait 2001].

Fieldwork was conducted between May 1998 and July 2000 in six Belgian and French coastal dunes complexes located between the cities of Nieuwpoort [Belgium, 51°08'N, 2°45'E] and Dunkerque [France, 51°03'N, 2°20'E] [Fig. III.5-1]. For the population genetic analysis, we additionally sampled dune habitat in the Boulonnais [France, 46°47'N, 1°19' E], the Zwin-estuary [Belgium, 51°22'N, 3°21'E] and in three areas along the Dutch coast: the Amsterdam Water Supply Dunes [52°22'N, 4°31'E], the dunes of the Provincial Water Company [52°38'N, 4°37'E] and the Isle of Terschelling [53°21'N, 5°12'E] [Fig. III.5-1]. Based on the habitat preference of *Pardosa monticola*, a total of 1100 ha of dune habitat were screened for the presence of the species during mid May and the first and second decade of June [1998 and 2000]. In 1998, a total of 95 habitat patches were selected. Of these, one occupied and one vacant patch became unsuitable in 2000 as a result of grass encroachment, and were therefore excluded from further analysis.

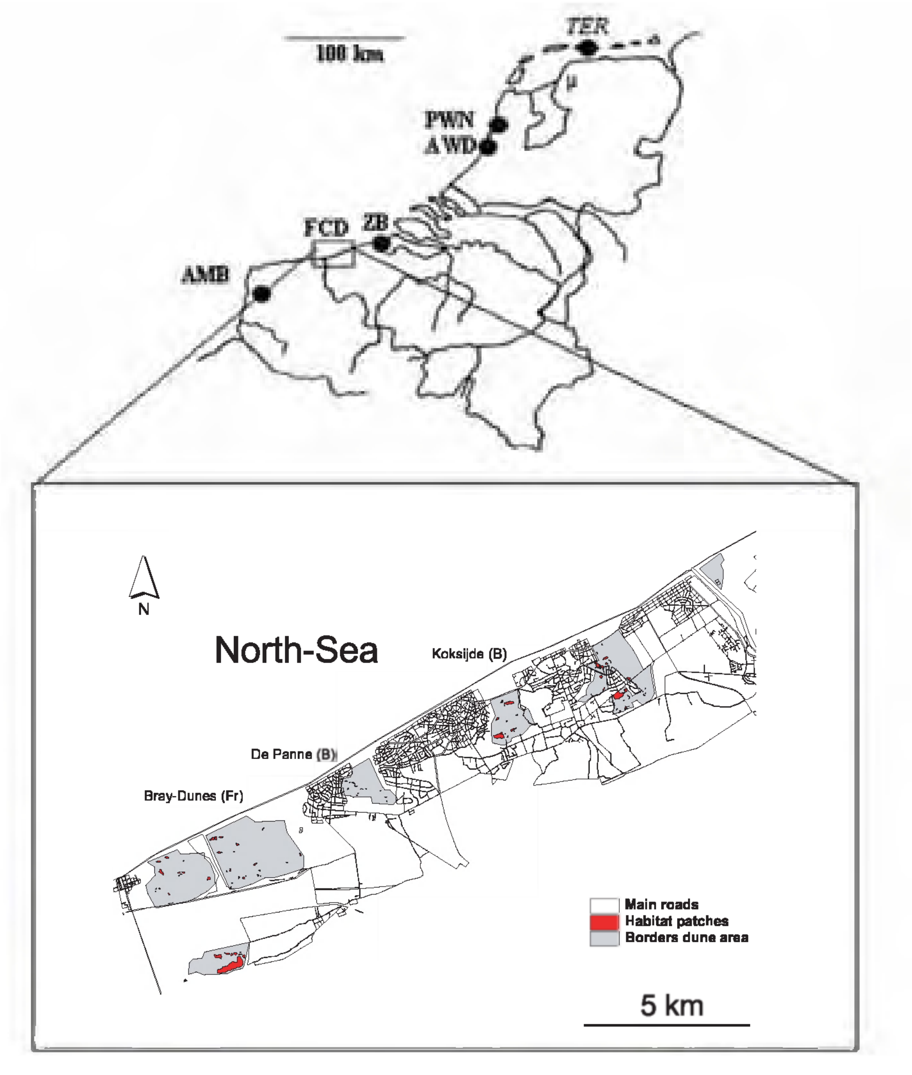

Fig. III.5-1: Location of the sampled populations for allozyme electrophoresis [upper] and patch location in the Flemish coastal dunes [under]. [AMB: dunes Ambleteuse; FCD: Flemish coastal dunes; ZB: Zwin estuary; AWD: Amsterdam water supply dunes; PWN: Provincial water supply dunes North-Holland; TER: Terschelling].

Dispersal

To estimate rates of mobility and potential effective realised distances in different habitat types, a total of 341 individuals were marked with a coloured paint spot at the caudal part of the prosoma and released in groups of a maximum of five individuals during the first decade of June 1998 [sunny conditions]. A total of 145 individuals were released in moss dunes with *Phleo-Tortuletum* vegetation, 120 individuals in moderately tall *Polygalo-Koelerion* grassland, and 76 individuals in tall and dense *Arrhenatherion* grassland. Twenty-four hours after release, the area was thoroughly searched for marked spiders, and distances from the respective releasing sites were measured. After fitting the frequency-data per distance of 2 meters, the proportion of dispersers per distance unit was calculated with the integral of the best fitting curve [non-linear regression]. Given that dispersal patterns on moss dunes and grassland are randomly orientated [Bonte *et al.*, unpub. data] and may hence obscure estimates of effective directional dispersal towards another patch, strait-line distances were calculated via goniometrical transformation. Based on these effective dispersal distance estimates and the proportion of individuals per distance class, we calculated the probability of daily dispersal distance. For two different vegetation types, daily dispersal probabilities were randomly combined for a 150-day dispersal period [i.e. reflecting approximate maximum female age] based on 10000 permutations.

Patch quality

Suitable habitat patches were digitised from aerial orthophotographs with a Geographic Information System [Arcview 3.1]. For each patch, we calculated patch area [ln-transformed to approach normality], proportion edge [i.e. contour/area ratio] and mean vegetation height [measured 20 times to the nearest cm with a polystyrene disk with diameter of 20 cm placed on a measuring rule, during the first week of July]. Patch size was included as a quality measurement since it has been shown to affect population size and viability [Bonte & Maelfait, unpubl. data]. Proportion edge, in turn, indirectly reflects the availability of suitable hibernating sites in the surrounding matrix [Bonte *et al.* 2000a].

To calculate a patch-specific index of habitat quality, we included the above measurements as independent variables in a stepwise forward multiple logistic regression model with logit[p]=ln[p/[1-p]] as dependent variable, whereby p reflects the probability of finding an occupied patch during at least one survey year. Chi-square statistics and changes in likelihood [-2 ln LL] were used respectively for entering [$P < 0.05$] and removing [$P < 0.01$] each of the independent variable in/from the model.

Patch connectivity

Based on digital aerial photographs and ground surveys, the vegetation type surrounding each habitat patch was scored as moss dune, Marram dune [blond dune with *Ammophila arenaria*], grassland, shrub, or woodland. Aerial distinction between these vegetation types was based on vegetation-specific red [RED] and near-infrared [NIR] reflectance values [Provoost et al. 2002]. Since patch colonisation by *P. monticola* can occur both by female cursorial dispersal or juvenile ballooning, we used different values [parameter a, see below], describing the relationship between number of migrants and distance between patches, for both modes of dispersal and different vegetation types surrounding each habitat patch. Based on experimental estimates of cursorial dispersal [this paper], we assigned a=100 for unsuitable habitat [dense grassland, shrub, or woodland], a=5.3 for tall grassland, and a=2 for sandy- or moss-dominated matrices. Based on literature data on aerial dispersal [Thomas 1996], we assigned a=4 for ballooning, independently of the surrounding matrix type. Connectivity estimates based on cursorial dispersal and aerial dispersal are referred to as $S_{fem.}$ and $S_{balloon}$, respectively.

Based on these data, patch connectivity was estimated as $S_i = \sum_{j \neq i} \exp[-\alpha d_{ij}] N_j$ [Hanski 1999a,b] with α = constant describing the strength of the inverse relationship between numbers of migrants from patch j and distance between patches, and N = population size at patch j [1 in case of occupancy; 0 in case of vacancy]. High values of S thus reflect high levels of connectivity. Together with the indices of habitat quality [see higher], patch connectivity indices were included as independent variables in a stepwise forward multiple logistic regression model with following patch characteristics as dependent variables: [i] occupancy status in 2000 [1 occupied; 0 vacant]; [ii] colonisation status in 2000 of patches vacant in 1998 [0 still vacant; 1 colonised]; and [iii] extinction status in 2000 of patches occupied in 1998 [0 still vacant; 1 extinct].

Population genetics

During spring and summer 1998 [Flemish coastal dunes] and 1999 [other populations], we collected between 30 and 65 individuals [exceptionally 17 from Terschelling] from 10 sites in the Flemish coastal dunes and five reference sites in Flemish, French and Dutch dune complexes [as indicated in Fig. III.5-1]. All individuals were captured by hand and transported alive to the laboratory, where they were frozen in liquid nitrogen and stored at –180°C. Electrophoresis was conducted following the method outlined in Hebert & Beaton [1989], using TRIS-glycine and TRIS-maleate as buffers [Richardson et al. 1986]. The following six enzymes, encoded by seven genetic loci, were analysed: fumerate hydratase [FUM, E.C. 4.2.1.2], asparate aminotransferase [AAT, E.C. 2.6.1.1], lactate dehydrogenase [LDH, E.C. 1.1.1.27] and malate dehydrogenase [MDH-1 and MDH-2. E.C. 1.1.1.37] [with TRIS-glycine as buffer] and isocitrate dehydrogenase [IDH, E.C. 1.1.1.42] and glucose 6-phosphate isomerase [PGI, E.C. 5.3.1.9] [with TRIS-maleate as buffer].

Electrophoretic data were analysed with software packages TFPGA [Miller 1997] and GENEPOP [Raymond & Rousset 1995]. Analyses either included all loci [for estimation of heterozygosity] or 95% polymorphic loci only [for estimation of population differentiation]. Genotype frequencies were tested for Hardy-Weinberg equilibrium both with exact significance probabilities [Miller 1997] and through global tests across loci [Raymond and Rousset 1995]. The degree of inter-population differentiation was analysed by calculating Nei's [1972] F_{ST}-statistics, which have been shown not to relate to gene flow [Nm] in realistic structured populations [Whitlock & McCauley 1999]. To examine isolation-by-distance effects, we regressed Nei's [1972] original genetic distance values to a matrix of kilometric distances between the populations, with the use of a Mantel test [Mantel 1967]. The relation between indices of habitat quality, connectivity and expected heterozygosity was examined by Spearman correlation coefficients.

Results

Dispersal

Average daily dispersal distances of marked individuals were 7.96 ± 6.95 m on moss dunes and 2.81 ± 1.96 m in grasslands [$F_{1,261}=103.7$; $P<0.0001$]. Mean dispersal distances did not differ between males and females [$F_{1,261}=3.2$; $P=0.071$], hence estimates were pooled for further analysis. Frequency distributions of individual dispersal distance were described by $f[x]=-1.706+43.443/x-98.871/\chi^2+56.860/\chi^2$ [$r^2=0.676$, $P<0.001$] for moss dunes and $f[x]=-1.317+23.332/x-14.636/\chi^2$ [$r^2=0.803$, $P<0.001$] for grasslands. Transformation to maximum effective direct straight-line distances yielded estimates of 280 m for moss dunes and 185 m for grasslands [Fig.

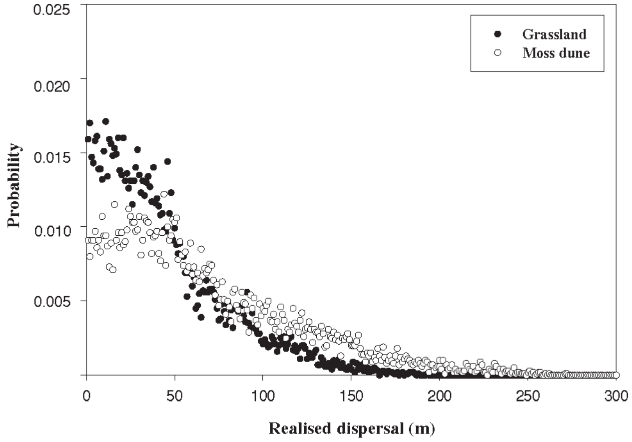

Fig. III.5-2: Estimated dispersal of female Pardosa monticola on moss dunes and grassland, based on extrapolation of spider mark-recapture data.

III.5-2].

Patch quality

A total of 53 patches were vacant during both survey years, 19 patches were occupied during one year, while the remaining 21 patches were occupied during both census years [Table III.5-1]. Vegetation height per patch did not differ between years [repeated measures ANOVA: $F_{1,1767}=0.1$; $P>0.05$]. The probability of a given patch being occupied in census year 2000 was significantly affected by ln[patch area] [$\chi^2_1=16.8$; $P<0.001$] and vegetation height [$\chi^2_1=17.5$; $P<0.001$], but not proportion of edge [$\chi^2_1=0.115$; $P>0.05$]. The logistic model Logit[*p*]= -16.550 + 1.476[patch area] + 0.338*[vegetation height] correctly classified 79.6% of all occupancy scores. Based on this model, a quality index ranging from 0.0001 to 0.9917 was scored for each patch.

Table III.5-1 - Habitat and connectivity characteristics of the patches in relation to their occupancy frequency [means with standard deviation].

	Never	**Once**	**Twice**	
n		53	19	21
Height vegetation [cm] 1998	12.557 [4.162]	14.541 [4.049]	15.102 [3.238]	
Height vegetation [cm] 2000	11.887 [4.243]	15.043 [3.676]	14.508 [2.508]	
Surface [m^2]	1567.981 [4077.239]	2014.263 [3176.991]	9886.524 [23870.822]	
Contour [m^{-1}]	0.295 [0.267]	0.208 [0.116]	0.130 [0.102]	
Index of habitat quality	0.269 [0.219]	0.552 [0.279]	0.727 [0.259]	
Ln[Sfem]	6.169 [2.700]	7.816 [1.892]	8.693 [2.337]	
Ln[Sballoon]	6.698 [1.824]	7.734 [2.019]	8.762 [2.309]	

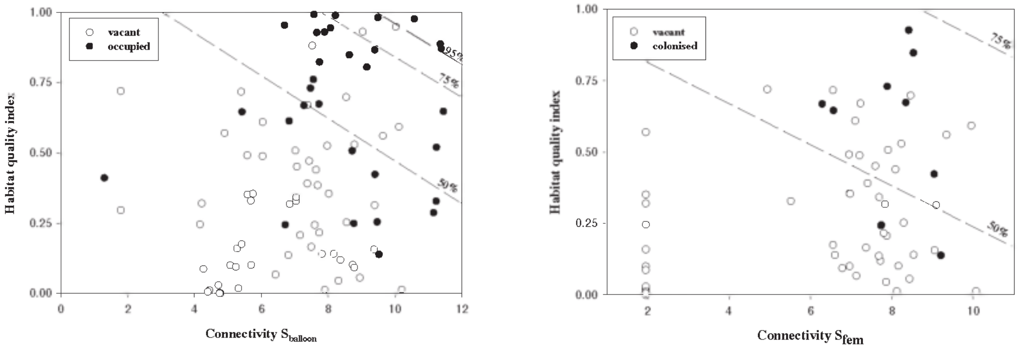

Fig. III.5-3: Patch occupancy [c^2=38.559; P<0.001; above] and colonisation probability [c^2=18.027; P<0.001; under] as related to the patch connectivity estimates [based on aerial dispersal [ballooning] [Sballoon] and female cursorial dispersal [Sfem]] and habitat quality index [HQI].

Patch occupancy

Patches that were occupied during zero, one or two census years differed significantly in habitat quality [$F_{2,90}$=30.2, P<0.0001], whereby patches with zero occupancy showed significantly lower habitat quality scores than the two other occupancy classes [Table III.5-1; Post-hoc Scheffé-test, p<0.001]. Connectivity estimates also differed in relation to patch occupancy [S_{fem}: $F_{2,90}$=8.8, P<0.001; $S_{balloon}$: $F_{2,90}$=8.6, P<0.001], whereby patches with zero occupancy were characterised by lower levels of connectivity than patches occupied during both census years [Table III.5-1; Post-hoc Scheffé-tests for S_{fem} and $S_{balloon}$, all P<0.001]. Patch connectivity was positively correlated with the patch quality index [S_{fem}: r_{93}=0.422; P<0.001; and $S_{balloon}$: r_{93}=0.310; P<0.005].

In a logistic regression model with occupancy status in 2000 [$n_{occupied}$=40; n_{vacant}=53] as response variable, both patch quality [χ^2_1=21.248; P<0.001] and $S_{balloon}$ [χ^2_1=18.080; P<0.001] significantly explained variation in occupancy [Fig 3]. The logistic model Logit[*p*]= -5.921 – 4.312[patch quality] – 0.297[$S_{balloon}$] predicting occupied patches in 2000 correctly classified 81.7% of all patches. Colonisation status in 2000 of patches vacant in 1998 [$n_{colonised}= 10$; $n_{vacant}=53$] was significantly explained by patch quality [$\chi^2_1=11.805$; $P<0.001$] and S_{fem} [$\chi^2_1=6.222$; $P<0.001$]. A logistic model Logit[p]= 3.777 – 1.051[patch quality] – 0.429 [S_{fem}] predicting the probability of colonisation in 2000 correctly classified 87.3% of all patches [Fig. III.5-3b]. Neither patch quality [$\chi^2_1=1.452$; $P>0.05$] nor patch connectivity [$S_{balloon}$: $\chi^2_1=0.276$; $P>0.05$; S_{fem}: $\chi^2_1=0.125$; $P>0.05$] explained the pattern of extinction in 2000 of patches occupied in 1998 [$n_{extincted}=9$; $n_{occupied}=21$].

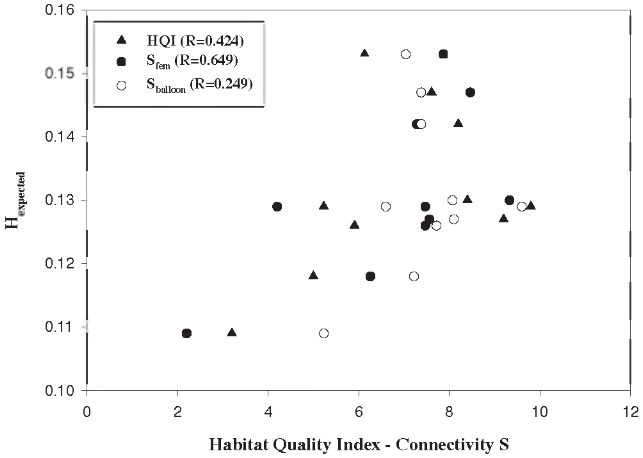

Fig. III.5-4: Relation between genetic diversity [Hexpected] and the habitat quality index [HQI], connectivity for cursorial [Sfem] and ballooning [Sballoon] dispersal for 10 patches in the Flemish coastal dunes. Rank correlation is only significant between Hexpected and Sfem [P=0.042]. For abbreviations, see Fig. III.5-3.

Population genetics

Genetic differentiation between the Flemish, French and Dutch populations was low [$F_{ST}=0.011$; SE=0.0033]. Inter-population differentiation was significant [$c?_8=40.913$; $P<0.001$], but only for 20% of all pairwise comparisons. In total, seven of the fifteen populations were not differentiated from each other [pairwise exact tests, with Bonferroni corrections, $P<0.004$]. No significant isolation by distance was observed [Mantel test, r=-0.167; $P>0.05$].

Overall, levels of genetic variability were moderate to low with a mean expected heterozygosity of 0.135 ± 0.022 [range 0.109-0.198]. At the scale of the Flemish west-Coast, levels of expected heterozygosity were marginally positively correlated with levels of S_{fem}, but not with $S_{balloon}$ and patch quality [Fig. III.5-4].

Discussion

The spatial distribution of *P. monticola* across suitable habitat patches was primarily related to patch quality, and to a lesser extent to patch connectivity as estimated for ballooning dispersal. The probability of short time colonization of a patch was both affected by its quality and its level of connectivity as estimated from cursorial dispersal rates. Patterns of local extinction, in contrast, were not related to patch quality or connectivity, and therefore appeared to be mainly stochastic.

Patch quality depended both on the structure [grass height] and size of the habitat patches. Because rates of juvenile mortality in wolf spiders are very high [*e.g.* up to 80% for *Pardosa lugubris*; Edgar 1971], the viability of subpopulations will largely depend on population size, which relates to patch size in *P. monticola* [Bonte, unpubl. data].

Patch-based indices of habitat quality were significantly correlated with those of connectivity, suggesting that high-quality patches [i.e. not too short grasslands] were clustered in space. Likewise, patches of low quality were clustered and poorly connected, due to the presence of dense shrubs. Higher levels of cursorial mobility in short than in tall vegetation types, as evident from the dispersal experiment, may have two non-exclusive causes. First, taller vegetation types may effectively hinder movement, as has been shown for darkling beetles [Criest & Wiens 1995]. Second, higher dispersal activity in the scarcely vegetated grey dunes may be due to a lack of suitable prey, such as epigeic springtails and Diptera [Bonte *et al.* 2002e; unpubl. data]. Likewise, Kreiter & Wise [2001] showed increased mobility in the absence of suitable prey for American populations of the fishing spider [*Dolomedes triton*]. Female spiders live two to three months longer than their male conspecifics and are founders. The dispersal pattern is however diffuse-like, so although fairly large distances can be covered during one day, the straight-line directive distance [1.86 meter/day] is averagely low, even in the best conductive habitat. In addition, we do not know whether the patch emigration rate changes during the season as demonstrated for other invertebrates [Isaacs & Byrne 1998; Albrectsen & Nachman 2001; Bellamy & Byrne 2001]. The inclusion of these detailed empirical dispersal data should result in better connectivity measures and in biologically more realistic metapopulation models.

Based on the above, the population structure of *P. monticola* in the Flemish coastal dune-complex resembles that of a metapopulation. Strong variation in patch quality, such as documented for size, structure, and connectivity, may give rise to source-sink dynamics [Dias & Blondel 1996]. Occupancy of sinks, which lay outside the fundamental niche of species, can be expected to depend directly on their dispersal ability and immigration rate [Boughton 1999]. In our study, connectivity additionally explains occupancy and colonisation patterns, indicating that the metapopulation structure of *P. monticola* in coastal dunes primarily depends on the habitat quality, as is the case for source-sink dynamics. The fact that apparently obvious metapopulations are affected by habitat quality was demonstrated by Briers & Warren [2000] for *Notonecta* backswimmers in ponds. Their results showed that considerable non-spatial correlated variation in habitat quality exists and that population turnover was driven by these quality dynamics. Moilanen & Hanski [1998] and Gutiérrez *et al*. [1999] failed however to improve the overall explaining power for a butterfly metapopulation by including environmental factors. The underlying mechanisms explaining the observed patch occupancy in fragmented habitats are hence dependent of the model organism. In our study, the ballooning-connectivity was the best additional predictor for patch occupancy, while colonisation processes at short term depended on the connectivity by cursorial dispersal. This is concordant with the findings of Bonte & Maelfait [2001], who showed that the ballooning capabilities of *P. monticola* under laboratory circumstances where very low [between 5-10%] and only occurred after starvation. At longer time spans ballooning can, however, be a successful colonisation mechanism since our observed occupancy pattern results from dispersal events at longer time intervals.

The low level of genetic diversity in *P. monticola* was in concordance with patterns observed in other dune dwelling arthropods [Ramirez & Froehlig 1997; Boulton *et al.* 1998], suggesting similar environmental selection pressures. According to Boulton *et al.* [1998], repeated sand overblowing events during the landscape genesis may have caused repeated genetic bottlenecks in coastal dune populations of several arthropod species. This may be especially true for *P. monticola*, which prefers a subclimax vegetation [short grasslands] that can easily be altered by either over- or undergrazing. The strikingly high level of heterozygosity in population PWN, an area characterized by a historically stable grazing regime [Doing 1988] confirms this hypothesis.

Estimates of genetic differentiation did not complement the spatial distributional pattern of *P. monticola* in the study area: whereas direct estimates of [cursorial] mobility indicated low levels of dispersal, low levels of genetic differentiation suggested high levels of gene flow [Whitlock & McCauley 1999]. Such discrepancy between genetic and distributional data may have different reasons. First, gene flow estimates based on F_{ST} may not reflect current levels of genetic exchange, but rather reflect historical patterns of interpopulation migration. Since large-scale fragmentation of Flemish coastal dune grasslands by urbanisation and shrub encroachment is fairly recent [i.e. less than 100 years], current low levels of genetic differentiation probably result from high levels of gene flow in the recent past. Alternatively, weak genetic differentiation may result from [infrequent] long-range dispersal via ballooning. In the latter case, however, some geographic pattern in genetic differentiation could be expected, given that the coastal populations of *P. monticola* were almost linearly orientated. The lack of an isolation-by-distance effect therefore suggests that historical gene flow, in combination with recent fragmentation of coastal dune habitat, caused the present patterns of weak genetic differentiation. Our study thus confirms the need for both direct and indirect estimates of dispersal when aiming to interpret current patterns of genetic differentiation [see also Peterson *et al.* 2001].

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III.6 EVOLUTION OF BALLOONING BEHAVIOUR IN A WOLF SPIDER INHABITING DIFFERENT DUNE LANDSCAPES


FOTO: DRIES BONTE

BONTE D., VANDEN BORRE J., LENS L. & MAELFAIT J.-P. ***Submitted to Evolution***

Abstract

Theoretical studies on the evolution of dispersal demonstrate that mechanisms related to habitat and population structure are important in shaping inter- and intraspecific variation. Empirical evidence for these relationships is however scarce. We address the relationship between habitat quality and dispersal by studying variation in tiptoe behaviour in the dune wolf spider Pardosa monticola, inhabiting grassland habitats differing in connectivity and predictability. This behaviour prepares spiders for passive aerial flight i.e. attached to a silk thread and carried by air currents [ballooning]. Offspring from field-captured females carrying eggsacs, were tested under standardized laboratory conditions. Our experiments revealed that postnatal proximate effects [starvation], prenatal maternal effects and innate effects influence the performance of tiptoe behaviour and that habitat fragmentation led to a decrease in dispersal rates, possibly because genes, associated with dispersal would disappear in isolated populations. Because maternal condition and fitness decrease with an increasing degree of patch isolation, selection against aerial dispersal may enhance a mechanism of risk spreading. Within one population, habitat quality influences offspring dispersal in an opposite way, and acts as a rescue effect for offspring in case the maternal habitat is of lower quality, resulting in a lower residual offspring size. As a consequence, behavioural traits narrowly linked to dispersal can evolve towards less mobile phenotypes in fragmented terrestrial habitats. The genetic basis of ballooning dispersal remains, however, to be unambiguously demonstrated by studies controlling for both pre-and postnatal conditions, but even if only maternal effects are involved at small geographic scales, they appear to be the most adaptive response since they use information from environmental variations more completely and lead to optimal dispersal strategies in function of the habitat quality and predictability.

Keywords: behaviour, dispersal, habitat, *Pardosa monticola*, maternal condition

Introduction

In contrast to winged arthropods, which have active flights, wingless arthropods disperse passively by air currents or other locomotion types. This ballooning dispersal is known from spiders and several other arthropod groups and is initiated by behavioural adaptations [*tiptoe*-behaviour] that enable the individual to take-off in the air: a spider climbs to an elevated starting point, stretches its legs and raises its abdomen; then it produces long silk threads and is finally carried up by the air current [Jones 1996a,b]. Ballooning dispersal is influenced by meteorological, proximate [environmental] and possibly by innate [ultimate] factors [Weyman *et al.* 2002; Bonte *et al.* 2003b]. Ballooning dispersal is associated with low wind velocities and result in fairly small dispersal distances [from a few meters up to a few 100 meters [Morse 1993; Thomas 1996; Compton 2002], depending on the number of repeated flights [Thomas *et al.* 2003]].

Interdemic or geographical variation in ballooning behaviour has not yet been demonstrated. Bonte *et al.* [2003b] studied the genetic and environmental background of tiptoe latency and detected biological meaningful variation underlying this behavioural trait, although they were not able to distinguish between additive genetic and maternal effects. In analogous studies on the ballooning latency in the [phytophagic] mite *Tetranychus urticae*, the additive genetic component was estimated to be more than 20% [Li & Margolies 1993,1994]. These findings stress the importance of genetic components in the expression of behavioural traits narrowly linked to dispersal. Besides genetic background, environmental conditions are able to trigger dispersal directly as an immediate behavioural response, or indirectly by first altering the internal body condition which in turn triggers dispersal [Ims & Hjermann 2001]. If maternal effects are linked to internal conditions, a time lag will be present between the environmental cue and the expression of the dispersal trait. These maternal effects can be involved when phenotypic specialization for dispersal takes place at an early ontogenetic stage [during early juvenile development], and when offspring are not capable of perceiving cues from the external environment. In such scenario, a maternal link in the pathway of condition-dependent dispersal conveys information about the environment not yet accessible to the offspring [Ims

& Hjermann 2001]. These responses may help the offspring to successfully settle in their natal environment or to increase their likelihood of dispersal [De Fraipont *et al*. 2000]. Although maternal effects are often interpreted as a non-genetic form of heredity [Sorci *et al*. 1994], they can be evolutionary significant if genotype and environment strongly correlate and maternal effects increase offspring fitness, or when maternal effects differ between genotypes [Mousseau & Fox 1998; Mazer & Damuth 2001]. For aerial dispersal, involving high survival costs, maternal effects could be a mechanism to preadapt offspring to the selective environment they are likely to encounter. The prevalence of the local adaptation hypothesis can hence be expected [Brody & Lawlor 1984; McGinley *et al*. 1987; Sorci *et al*. 1994].

Although both population genetics and quantitative genetics have demonstrated extensive geographic variation in non-behavioural traits [Foster 1999], evolutionary studies on geographic variation in behaviour are scarce despite the fact that they may offer best hope for dissecting the causes of behavioural evolution [Arnold 1992; Foster 1999]. Evidence for adaptive microevolution can be diagnosed in a trustworthy way within species if correlation exists with environmental factors that are presumed to cause selection and if analogous patterns are found in related species. Because population differences may reflect variation in experience with the habitat, common garden experiments should be used for the detection of additive or non-additive interdemic variation [Arnold, 1992]. Since geographic variation in behaviour can evolve over relative short time frames [Riechert 1999], population contrasts can be especially valuable to explore apparently adaptive differences among populations, because divergent populations might be separated for less time than higher taxonomic units and might therefore often reside in the habitats where the differences evolved [Endler 1986].

We here examine how the performance of tiptoe behaviour, as a measure of dispersal propensity, of *Pardosa monticola*-offspring varies between landscapes, that differ in the availability and connectivity of suitable grassland habitats, and whether it changes in function of the predictability of prey abundance in two contrasting maternal habitats within a single landscape type. Theoretical studies on the evolution of dispersal revealed that it is selected against by intrinsic costs and stable environmental heterogeneity [Holt 1985; Doebeli & Ruxton 1997; Parvinen 1999], while it is favoured by kin competition [Hamilton & May 1977; Perrin & Lehman 2001; Lehman & Perrin 2002], inbreeding avoidance [Chesser & Ryman 1986; Perrin & Mazalov 1999], temporal variability and decrease of habitat quality [Van Valen 1971; McPeek & Holt 1992]. Weak flyers will reach suitable habitat only by chance, suffer from high mortality, such that the number of individuals entering the population will be lower than the number leaving, especially when the parent population is isolated. Natural selection will thus favour individuals that stay behind in the parent population [Den Boer 1970]. When this occurs, genes connected to dispersal will only be maintained if recruitment in newly founded populations is sufficiently high to compensate for losses due to dispersal. This balance can shift in favour of local settlement if suitable habitats become more isolated or stable [Southwood 1962; Dieckmann *et al.* 1999].

Based on the above, we hypothesize that

- Ballooning propensity will be highest in offspring originating from open dune landscape, dominated by well-interconnected grasslands.

- Due to the fact that prey [Collembola] availability can be limited during summer droughts in grasslands, but not in humid dune slacks, and if maternal variation in offspring ballooning performance exists, we can suspect additionally that the predictability of the dune slack habitat selects against offspring dispersal.

- Prey deprivation triggers the propensity for aerial dispersal.

Material and methods

Study organism

The wolf spider, *Pardosa monticola* [Clerck, 1757], a widespread species in Europe and Asia, typically occurs in short and oligotrophic grasslands and heathland [Wiebes & Den Hollander 1974; Alderweireldt & Maelfait 1990]. In Flemish and Dutch coastal dunes, the species prefers grey dune grassland, grazed by rabbits and young dune slacks with a moderate vegetation coverage, where it is known to survive periods of flooding during winter [Van der Aart 1975; Maelfait *et al*., 1989; Bonte & Maelfait 2001]. Due to its regional scarcity, the species is listed on the Flemish Red List of endangered spiders [Maelfait *et al*. 1998]. During winter, *P. monticola* retreats in juvenile or subadult instars in rough, litter-rich vegetation. Males have been observed to diffuse cursorially on grey dunes with different amounts of bare sand [Bonte & Maelfait 2001]. In the Flemish coastal dunes, the species lives within a metapopulation, with habitat quality as measured by vegetation height and patch size being of primary importance in structuring the spatial population structure [Bonte *et al*., 2003c]. Short-term population dynamics are mainly predicted by cursorial dispersal, while patch occupancy, resulting from long-term colonisation-extinction dynamics, mainly results from aerial [ballooning] dispersal [Bonte *et al*. 2003c]. Nothing is known about the species' mating strategy in the field, but second mating events, although not common, were already observed under laboratory conditions [Bonte, pers. obs].

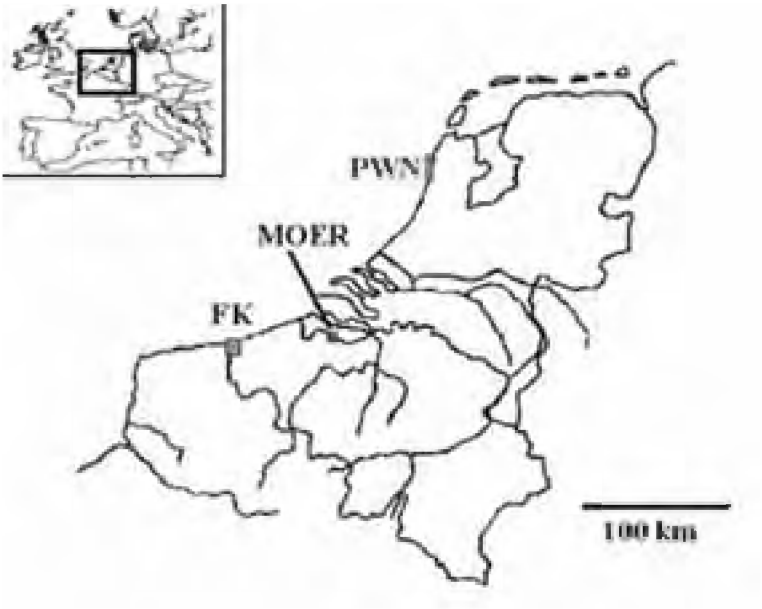

Fig. III.6-1: Location of the three different dune landscapes in which Pardosa monticola were sampled. PWN: North-Holland dune reserve [open landscape]; FK: Flemish coast [intermediate landscape] and MOER: Moerbeke-Heidebos [closed landscape]

Study site

Female spiders with attached eggsacs were collected in dune grassland from three different dune landscapes: North-Holland dune reserve [Netherlands, Bergen-aan-zee, 52°38'NL, 4°37' EL], Flemish coastal dunes [Belgium, De Panne-Ghyvelde, 51°05'NL, 2°32' EL], and inland dunes of Moerbeke [Belgium, 51°11'NL, 3°55' EL] [see Fig. 1]. These grasslands belong to the *Cladonio-Koelerietalia* and are characterized by prey limitation for *Pardosa*-offspring during warm and dry summer weather [Bonte *et al.* 2002e]. In the Flemish coastal dunes, *P. monticola* also occurs in humid, yearly mown dune slacks. In contrast to dune grasslands, vegetation is dominated by low sedges [*Carex trinervis, C. flacca*], grasses [*Agrostis capillaris*] and low creeping willow *Salix repens* and prey are continuously and abundantly present due to the high humidity and the presence of mycorrhiza in the *Salix repens*-litter [Bonte, unpub. data].

These three landscapes differ in the degree of grassland configuration and are referred to as respectively the open, intermediate and closed landscape. The open landscape of the North-Holland dune reserve [NHD] is a 5300 ha-large dune complex, in which *Pardosa*-females were sampled in a well-connected grassland-shrub complex of 400 ha [Wimmenummerduinen near Egmond], situated around the historic sea-village landscape [Zumkehr, 2001]. The intermediate landscape of the Flemish coastal dunes is heavily fragmented, but large patches are well connected [Bonte *et al.* 2003c]. Mean patch size is 1.41 ha and habitat connectivity for ballooning dispersal is moderately high [Bonte *et al.* 2003c]. Two subpopulations were sampled in dune grassland [with areas of 0.95 and 1.3 ha and dune slacks with patch area of 0.33 and 0.39 ha. The population from the closed landscape in Moerbeke contains a strongly isolated and small [patch area of 0.48] population, situated within a hostile woodland matrix.

Estimation of ballooning propensity

Tiptoe behaviour was studied following Legel & Van Wingerden [1980] and Bonte *et al.* [2003d]. Spiders were placed on a plaster platform with vertical nails, in groups of five individuals as to reduce the level of intraspecific interaction. The frame was placed in a windtunnel with an upward current of 1-1.2 m/s at a temperature of 30 ± 2°C and an aerial humidity of 40-50%. To prevent cursorial escape, the frame was placed in water. Observations were conducted during 20 minutes. Observations of tiptoe behaviour of three seconds or more were considered valid [Bonte *et al.* 2003b]. Females, carrying eggsacs were collected in June-July 2001-2003. In total, 2039 observation on tiptoe behaviour were conducted. Offspring originated from 56 mothers [Moerbeke: 10; Netherlands: 10; Flemish coast: 11 and 10 from grassland habitat and 8 & 7 from dune slacks] and were tested in well-fed condition [Collembola *Sinella curviseta* prey at libidum] and after one-week starvation. Offspring were reared under laboratory circumstances of 20±2 °C and a 16:8 day/night light regime.

Maternal reproductive characteristics

Maternal size was assessed by female cephalothorax width and length measured under a 50x binocular microscope with measurement scale. Offspring cephalothoraxes were drawn under a 100x microscope with a drawing tube; their perimeter was determined after digitisation with *Summagraphics Summasketch III* as a measure of their size. Since preliminary results indicated that offspring size did not significantly differ between ballooning and non-ballooning offspring of the same clutch [Vanden Borre unpub. data], mean offspring size was determined for each clutch. Because clutch size [r_{53}=0.57; P<0.001] and mean offspring size [r_{53}=0.41; P<0.001] covaried strongly with maternal size over all the populations, size was retained in the statistical models [see below] until covarying parameters were backwards eliminated. By this procedure, and in contrast to the use of residuals of offspring and clutch size as independent parameters to maternal size, unbiased parameter estimates were obtained [Freckleton 2002]. Maternal size can hence be considered as a measure of ‘absolute fitness’, while reproduction characteristics correspond to ‘relative fitness’ measures.

Statistical analyses

Variation in maternal size, offspring size and clutch size in the three landscapes [grasslands only] was tested by one-way ANOVA with population as fixed factor. Differences between grassland and dune slack habitats [intermediate landscape only] were analysed with a mixed model with habitat as fixed factor and subpopulation as nested random factor. Because maternal fitness characteristics covaried in the same way as tiptoe frequency between the sampled populations from the different landscapes [see results], they were only included into the analysis to investigate differences and variation in the frequency of mothers with ballooning offspring between the two habitat types and subpopulations within the intermediate landscape.

Logistic models [logit link] with individual tiptoe-performance [0/1] or presence of tiptoeing offspring within the maternal clutch [mothers without offspring performing tiptoe behaviour were scored as 0, those with tiptoeing offspring as 1] as dependent variables were used to test the hypotheses concerning variation in dispersal propensity. We will respectively refer to both types of models as the individual- and the clutch-based logistic model. Variation in tiptoe performance between the three landscape types was tested for the grassland populations with both types of logistic models. The total number of tested spiderlings was included as covariable in clutch-based model. The factor '*clutch*, nested within the landscape type, was included as random variable in the individual-based model.

Both types of logistic models were used to analyse variation between habitat types, in function of the maternal condition. Habitat type [grassland versus dune slack] and maternal fitness characteristics [clutch size, mean offspring size and maternal size] were included as fixed factors. Both subpopulations were nested as factor within the habitat type. As in previous analysis, factor '*clutch* was nested as random factor within the subpopulation in the individual-based model and the total number of tested spiderlings was included as covariable in the clutch-based model.

The effect of starvation on tiptoe performance was tested for offspring from the open population with the individual-based logistic model. Data on individual performance were analysed as repeated measures and factors '*clutch*' and the interaction with starvation treatment were included as random variables.

All logistic models were tested against the χ^2 distribution [df=1] of the Log-Likelihood-difference between models with and without the variable of interest. The degrees of freedom were approximated using Satterthwaite's procedure. A backwards elimination of the non-significant parameters was performed in the multiple models [glimmix procedure in SAS 8.1].

Results

Interdemic variation in maternal fitness characteristics

Maternal size [$F_{2,36}=12.21$; $P<0.0001$], offspring size [$F_{2,31}=12.16$; $P<0.0001$] and clutch size [$F_{2,36}=9.93$; $P<0.0004$] differed significantly between grassland populations from the three landscape types [Table III.6-1]. For all traits, values for the open landscape were significantly higher than those for the intermediate and closed landscape. Differentiation in fitness characteristics was non-significant between habitat types and between the subpopulations, nested within the intermediate landscape [maternal size: $F_{1,2}=0.38$, $\sigma^2_{subpopulation}=34348$; offspring size: $F_{1,2}=0.11$, $\sigma^2_{subpopulation}=0.01$; clutch size: $F_{1,2}=1.12$, $\sigma^2_{subpopulation}=10.88$; All $P>0.05$].

Table III.6-1 - Mean values [±sd] of maternal size, offspring size and clutch size for six study populations from three different landscape types, including the different subpopulations in the intermediate landscape.

	open	intermediate				closed
		Grassland1	Grassland2	Slack1	Slack2	
Maternal size [mm^2]	5009.30 ±507.31	4092.64 ±499.34	3213.00 ±311.43	4546.37 ±483.70	4042.57 ±568.06	4219.20 ±669.56
Offspring size [mm]	2.48 ±0.10	2.33 ±0.07	2.35 ±0.10	2.34 ±0.06	2.36 ±0.04	2.28 ±0.09
Clutch size	44.10 ±10.20	27.75 ±12.55	21.63 ±10.90	36.87 ±29.71	24.85 ±19.74	27.50 ±7.87

Interdemic variation in ballooning propensity

Effects of landscape structure

Variation in tiptoe behavior frequency among offspring from grasslands of the three landscape types, was significantly affected by the landscape structure [$F_{2,46.7}=5.01$; $P=0.011$; see Fig. 2]. Ballooning propensity was lowest in the closed landscape [0.53 %, range 0-9.1%] and significantly lower than in the intermediate [8.30%, range 0-27%] and open dune landscape [11.32%, range 0-36.6%]. Variation between clutches within each landscape was significant [$\sigma^2=0.3664$; $\chi^2_1=105.8$; $P<0.0001$; residual variance 0.807]. The model was significantly robust [$\chi^2_{664.05}$=289.27 P>0.05].

Likewise, the frequency of clutches with tiptoeing offspring differed between grasslands from the three landscapes [$F_{2,36}$=4.18; P=0.023] and was independent of the number of spiderlings tested [$F_{1,35}$=0.89; P=0.353].

Estimated frequencies of clutches with ballooning offspring were lowest in the closed landscape [10.0 %, range 3.7-33.9%] and significantly lower than those from the intermediate [63.15%, range 36.4-83.7%] and the open dune landscape [90.00%, range 84.57-93.66%].

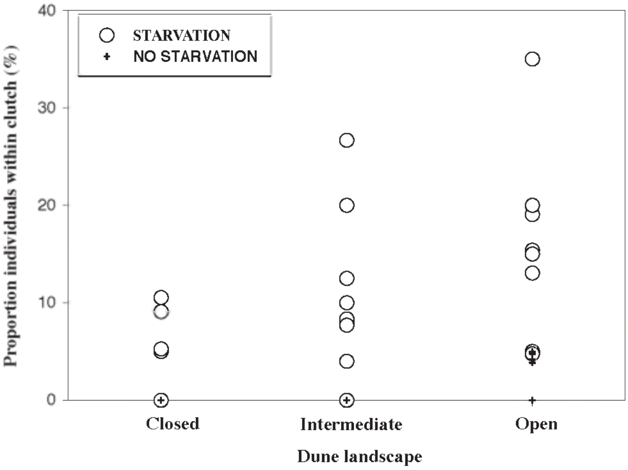

Fig. III.6-2: Proportion individuals per clutch performing tiptoe behaviour in relation to landscape connectivity.

Effects of habitat type

Variation in tiptoe behaviour frequency between clutches from the grasslands and dune slacks in the Flemish coastal dunes, differed significantly between both habitat types [Table III.6-2; Fig. III.6-3]. Tiptoe frequency in offspring from grassland was higher [8.30%, range 0-27%] than in offspring from dune slacks [0.3%, range 0-7.7%]. Variation between clutches and between the two subpopulations within each habitat type was significant [Table III.6-2]. Residual variance equaled 0.784. Deviance of the model was not larger than expected by chance [χ^2_{532}=165.95; P>0.05].

Variation due to habitat type in the former model was explained by maternal fitness in the clutch-based logistic model, more specifically by the interaction between clutch size and offspring size, controlled for maternal size [Table III.6-2]. Mothers with a low residual clutch size and constant offspring size had higher chances to hatch tiptoeing offspring than those with a higher residual clutch size, trading-off against offspring size [Fig. III.6-4]. Additional variation in the frequency of clutches with tiptoeing offspring was explained by factor subpopulation. The model fitted significantly well [$\chi^2_{36}=38.01$; $P>0.05$].

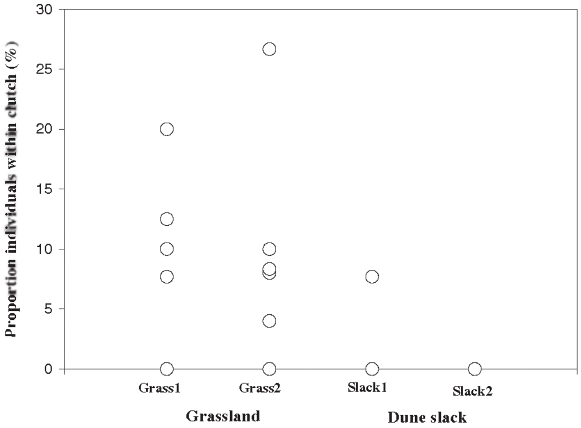

Fig. III.6-3: Proportion individuals per clutch from the intermediate landscape performing tiptoe behaviour after starvation, in relation to habitat type.

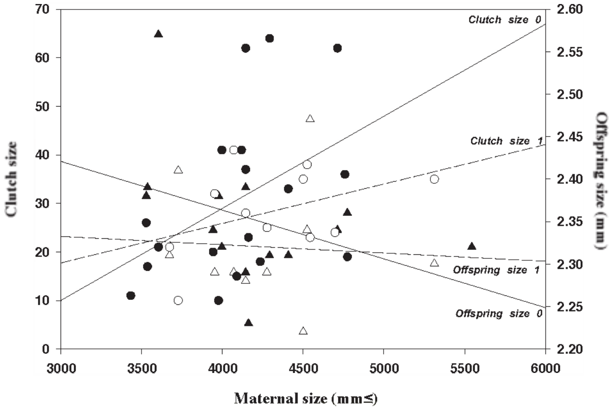

Fig. III.6-4: Relation between reproductive output [circles: clutch size; triangles: mean offspring size] and maternal size for mother with [open symbols] or without [filled symbols] tiptoeing offspring within their clutch.

Table III.6-2 - Logistic model for tiptoe frequency of offspring within clutches and for clutches with or without ballooning offspring, in function of the habitat type [grassland versus dune slack], maternal fitness characteristics and the subpopulation.

Tiptoe frequency of offspring within clutches				
Variable [Fixed]	**Num df**	**Den df**	**F**	**P**
Habitat type	1	20.9	10.19	0.004
Maternal size	1	13.2	1.82	0.201
Number of offspring	1	30.5	1.00	0.324
Mean offspring size	1	15.1	1.26	0.278
Number of offspring x mean offspring size	1	17.2	1.80	0.197
Variable [Random]		≈	**c≈1**	**P**
Clutch [subpopulation]		0.259	118.3	<0.001
subpopulation [Habitat]		0.090	6.4	0.005
Frequency of clutches with ballooning offspring				
Variable [Fixed]	**Num df**	**Den df**	**F**	**P**
Total offspring tested	1	11.1	0.74	0.407
Habitat type	1	2.89	4.99	0.115
Maternal size	1	15.1	3.14	0.026
Number of offspring	1	15.4	5.69	0.304
Mean offspring size	1	15.3	3.76	0.071
Number of offspring x mean offspring size	1	15.4	5.70	0.030
Variable [Random]		σ^2	χ^2_1	**P**
Subpopulation		5.9	4.6	0.026

Effects of starvation

Variation in tiptoe frequency among offspring from the open landscape was affected by the degree of starvation to which they were subjected [Table III.6-3]. Mean tiptoe frequencies within clutches were 14.43% after a one-week period of starvation and 2.90% after a week of high prey availability. Variation within clutches and the covariate structure were highly significant [Table III.6-3], indicating that tiptoe performance after starvation was additionally dependent on the clutch and the individual performance after a period of food excess. The model was significantly robust [$\chi^2_{556.66}=226$; $P>0.05$]. Residual variance [σ^2] was estimated to 0.702.

Table III.6-3 - Logistic model for tiptoe frequency with the degree of starvation, fitness characteristics and their two-way interactions as fixed dependent effects.

Variable [Fixed]	Num df	Den df	F	P
Starvation	1	291	17.78	<0.0001
Variable [Random]		σ^2	χ^2_1	**P**
Mother*Starvation		0.001	0.006	0.938
Mother		0.188	19.3	<0.0001
Covariate structure		0.217	23.1	<0.0001

Discussion

To study geographical and interdemic variation in *tiptoe* performance, a behavior known to initiate aerial dispersal in spiders, *Pardosa monticola* offspring from grasslands of landscapes differing in their degree of patch area and connectivity [an open, intermediate and closed landscape] were reared and tested under standardized laboratory conditions. We additionally sampled females from two habitat types in the intermediate landscape, with different predictabilities of prey abundance. Offspring were tested under well-fed and starved conditions. Because we observed low tiptoe frequencies in general and no tiptoe behavior by offspring from the intermediate and closed landscape under well-fed conditions, we tested for effects of starvation, landscape configuration and habitat predictability in three separate analyses. Our results confirm the positive effect of acute starvation on tiptoe behavior [Van Wingerden & Vugts 1974; Legel & Van Wingerden 1980; Weyman & Jepson 1994; Weyman *et al*. 1994; Weyman *et al.* 2002 and Bonte *et al.* 2003b. The covariate structure, although significant, must be interpreted cautiously due to the dominance of individuals which did not perform tiptoe behavior in both treatments and is hence of low biological relevance.

At the landscape-scale, the performance of tiptoe behaviour appears to be counterselected in small and isolated grassland habitats. Offspring from open landscape showed the highest level of tiptoe behaviour. At this geographic scale, the positive relationship between maternal fitness and offspring dispersal propensity results as a covarying reaction towards differences in habitat configuration as a quality-indicator. Within the intermediate landscape, substantial variation in ballooning propensity exists between the grassland and dune slack habitat type and between the sampled subpopulations. The frequency of tiptoeing spiderlings within each clutch appeared to depend only on the habitat type and the subpopulation, and confirms our hypothesis that high habitat predictability selects against dispersal performance. Whether potential ballooners are present within a clutch is, however, not directly related to the maternal habitat characteristics but to maternal fitness. Mothers without tiptoeing offspring have, relative to their size, a higher clutch size that trades off against offspring size, whereas mothers with tiptoeing offspring have a lower relative clutch size but constant offspring size.

Geographic variation in function of grassland configuration within dune landscapes is concordant with expectations based on selection against dispersal if chances of reaching suitable habitat are low [Bonte *et al*. 2003d]. Individuals inhabiting large grassland complexes are apparently fitter and more mobile than when inhabiting isolated and fragmented habitat remnants. At this geographical scale, selection potentially occurred for genes coding for or against ballooning, but maternal effects cannot *a priori* be excluded since only the F1-generation of spiderlings was tested.

The presence of females with ballooning offspring in different habitats and subpopulation interconnected by metapopulation dynamics [Bonte *et al*. 2003c] seems to be enhanced by maternal condition: females that have presumably experienced a lower [local] habitat quality will have a lower clutch size and relatively similar-sized offspring, which did not perform tiptoe behaviour within the time span of the laboratory test. Variation in tiptoe frequency within clutches, was not directly dependent on maternal condition, but follows the predictions of habitat predictability. One explanation might be that other maternal effects like egg-quality trigger the proportion of fast reacting spiderlings under laboratory circumstances. Individual variation between and within clutches is consistent with a mixed Evolutionary Stable Strategy *sensu* Parker & Stuart [1976], in which each individual from a genetical monomorphic population selects a variable strategy from common probability distribution, with the possibility of fine adjustment according to environmental conditions, in our case also maternal conditions. A similar and apparently random variation [or better: unexplained residual variation] has been observed in other studies [Samu *et al*. 1996; Morse 1997].

According to Weyman *et al.* [2002], random switching is responsible for the observed variation in ballooning within populations, although some studies, especially in the field, do not correct for spatially and temporally variable environmental effects within populations.

The relationship between interdemic variation in tiptoe performance and the environment reveals the possibility of natural selection on the ballooning dispersal or on mothers, which trigger [or reduce] ballooning dispersal behaviour in their offspring. The expression of maternal environmental effects differs among genotypes within these populations, and indicates that the maternal effect has the potential to evolve [Mazer & Damuth 2001]. In strongly isolated populations, mothers, who do not enhance ballooning behaviour of their offspring, potentially increase their fitness by minimizing dispersal mortality. Mothers from the open landscape trigger their offspring to balloon in higher proportions, and hence benefit directly by reducing inbreeding [Chesser & Ryman 1986; Perrin & Mazalov 1999] or kin competition [Hamilton & May 1977 Perrin & Lehman 2001; Lehman & Perrin 2002]. The low proportions of ballooners within clutches could indicate that these benefits are relatively low, compared to direct fitness costs. Additionally, since clutch size is largest in the population from this landscape, the low numbers of fast reacting potential ballooners within each clutch can be selected in function of risk spreading [Kisdi 2002], as the majority of the offspring show no propensity to balloon within the short time span of observation. Likewise, large variation within clutches can result from selection of risk spreading within the population. Overall, potentially low fitness benefits by increasing offspring dispersal indicate that the adaptive maternal variation will be low. The adaptive value in restricting offspring dispersal can however be higher, since reducing dispersal may seriously increase fitness in isolated populations. Natural selection potentially acts asymmetrically and directionally on offspring ballooning propensity, independently of whether it is locally influenced by maternal effects.

Alternatively, selection may directly act on the dispersal behaviour. Possibly, the frequency of individuals performing the pre-ballooning tiptoe behaviour would increase and variation within and between clutches would decrease. However, as both the frequency of ballooning offspring within the clutches and the frequency of females with [at least one] ballooning offspring showed predicted differentiation in function of the habitat configuration, an adaptive value is almost certainly present, but we cannot distinguish whether selection acts directly or indirectly, via maternal effects, on the dispersal behaviour of the spiderlings.

Variation in offspring ballooning performance can also be genetically determined, without any adaptive origin, as genetic correlations with traits evolved as adaptations to the habitat or landscape type [Roff 1997; Mazer & Damuth 2001]. A correlation between genes coding for ballooning behaviour and for instance foraging activity, prey choice or parasite resistance may well exist, but is unlikely due to analogous selection pressures within the dune grassland habitats and the overall low genetic differentiation between populations, irrespectively of their geographic distance [Bonte *et al*. 2003c]. Due to the loss of pleiotropic or linkage interactions, genes coding for dispersal may become afunctional [Roff 1997].

The presence of significant variation between closely located [sub]populations in the intermediate landscape makes additive evolution at this small scale less likely, especially since the presence of ballooning individuals within the female offspring was related to maternal condition. These populations can, however, be isolated for a short term, as aerial dispersal appeared only to determine long-term patch occupancy patterns [Bonte *et al*. 2003c]. In this case, rapid interdemic microevolution for mothers, stimulating or restricting ballooning dispersal [as reflected in the frequency of ballooning offspring within each clutch] or adjusting the behavioural threshold to perform ballooning, may have occurred in function of habitat predictability.

Because females with a relative smaller clutch size had higher chances to hatch at least one ballooning spiderling [possibly by decreasing the threshold time span to perform pre-ballooning behavior], the observed interdemic pattern likely resulted solely from interaction with non-additive maternal variation over subsequent generations, as suggested by Bonte *et al.* [2003b]. This pattern contrasts to the observed positive covariation at the landscape-level between mean clutch size and ballooning propensity. Within the intermediate landscape, females that experienced a local low habitat quality trigger at least a small proportion of the offspring to disperse aerially. Similar maternal effects on the ballooning frequency within clutches from dune slacks and grassland were not found, so other maternal effects may have induced variation in ballooning frequencies within the restricted observation period. Possibly egg quality [lipids, proteins, hormones] can be influenced by the physiology of the mother, inhabiting different habitats and experiencing different environmental cues, as demonstrated in the gypsy moth [Diss *et al.* 1996] and results in different thresholds of offspring to perform the dispersal behaviour, in accordance with the previously mentioned "random" mixed ESS [Parker & Stuart 1976]. This apparently "random" strategy may hence be a cryptic environmental or evolutionary trigger that only appears to be random because of hardly detectable relationships with the [genetical] environment. Hence, variation in ballooning performance in subpopulations differing in habitat quality and predictability [Van Valen 1971; McPeek & Holt 1992], seems to be a maternal-conditional dependent dispersal [Ims & Hjerman 2001] and enables offspring, without experience of the environment, to react on environmental cues experienced by their mother.

Regardless of the nature of the evolutionary trigger for ballooning propensity, we demonstrate for the first time geographic and interdemic variation. In the past, only Richter [1971] found indications of variation in tiptoe-performance in spatially separated population, although his results could not be tested in a proper statistical way. Passive wind dispersal is not a solely characteristic for spiders, but common in plants, mites and butterfly larvae. A reduced dispersal propensity in weedy, short-lived and wind-dispersed plants of inshore islands in Canada has been detected by Cody & Overton [1996] and interpreted as a striking example of short-term evolution in small and isolated natural populations, although only phenotypic variance was studied. Similarly, dispersal propensity in lepidopteran larvae also showed considerable interdemic variation [Diss *et al.* 1996], but appeared to be associated with nutritional experience of the maternal population, but not with egg size and egg protein content. Whether additive variance contributed to the observed patterns, was not studied. Only Li & Margolies [1993; 1994] demonstrated the heritability of traits, related to wind dispersal in the mite *Tetranychus urticae*. In the saltmarsh-inhabiting carabid beetle *Pogonus chalceus*, patterns in wing development appeared to decrease with an increasing age of the saltmarsh [ranging from 50-7000 years], probably due to a continuous emigration of winged individuals [Desender *et al.* 1998]. In their study, however, the oldest and largest saltmarsh contained a large population of beetles with well-developed wings. Our findings support the tentative explanation of Desender *et al.* [1998] that the size of the saltmarsh selects against the loss of dispersal ability, because chances of reaching suitable habitat are high. In a similar, but much smaller-scaled study, Richter [1971] found no influence of habitat age on the dispersal propensity within offspring of *Pardosa amentata*-clutches, although clutches with extreme large proportions of ballooning spiderlings were found in a young population. Variation in offspring ballooning dispersal may hence result from the interaction between age and size of the habitat. As the grasslands within our studied landscapes are all older than 2000 years [Bonte *et al.* 2003a], selection in function of habitat age may, in contrast to selection in response to habitat size, be marginally important.

Conclusion

Our experiments revealed that postnatal proximate effects [starvation], prenatal maternal effects and innate effects influence the performance of tiptoe behaviour and that habitat fragmentation can lead to a decrease in dispersal rates, possibly because genes, associated with dispersal will disappear in isolated populations [Dieckmann et al. 1999]. Because maternal condition and fitness decrease with an increasing degree of patch isolation, selection against aerial dispersal enhances a mechanism of risk spreading: when habitat fragmentation leads to decreased reproductive output, the loss of dispersal will slow down the negative population growth because all offspring is retained within the population. In case reproductive output is higher, more offspring potentially disperse out of the native population, but will have a smaller effect on the population growth because of their relatively low frequency and the presence of sufficiently non-dispersers staying behind. Within one population, habitat quality may influence offspring dispersal in an opposite way, and act as a rescue effect for offspring in case the maternal habitat is of lower quality, resulting in a lower residual offspring size. As a consequence, behavioural traits narrowly linked to dispersal may in addition to the morphological design of species [and populations], evolve towards less mobile phenotypes in fragmented terrestrial habitats [Van Dyck & Matthysen 1999]. The genetic basis of ballooning dispersal remains, however, to be unambiguously demonstrated by studies controlling for both pre-and postnatal conditions, but even if only maternal effects are involved at small geographic scales, they appear to be the most adaptive response since they use information from environmental variations more completely and lead to optimal dispersal strategies in function of the habitat quality and predictability.

III.7

LACK OF HOMEWARD ORIENTATION AND INCREASED MOBILITY RESULT IN HIGH EMIGRATION RATES FROM LOW-QUALITY FRAGMENTS IN A DUNE WOLF SPIDER

FOTO: DRIES BONTE

BONTE D., LENS L. & MAELFAIT J.-P. *Journal of Animal Ecology*, in press

Abstract

Mobility and emigration were investigated for the wolf spider Pardosa monticola *in grey dune fragments from two high-density and one low-density population, where population density was related to patch quality. Pitfall trapping in combination with absolute quadrat sampling was applied. Orientation behaviour was additionally observed in the high- and low-density patches during two periods in the adult life-phase [mating and reproduction period]. Dune grassland is the core habitat; moss dominated vegetation is the matrix in which dispersal occurs.*

Our field experiments confirm the hypothesis that increased activities of a dune wolf spider in a low-density habitat result in higher emigration rates. The diffusive emigration rates, which are higher close to the patch border, and intrinsic mobility within the patch, are higher in the low-density population. In the low-density patch, females are even more active than males and emigrate in the same proportions as males. Both males and females were not able to orientate and perform homeward movements during the spring period, in which vegetation height is more or less equal in the core habitat [grassland] and the matrix [moss dune]. In June, no homeward orientation was observed in the habitat patch with low quality and low densities [low vegetation height]. In the high-density patch, females but not males were able to perform homeward orientation behaviour at distances close to the pronounced border between grassland and moss dune. At distances of three meters, females orientated again randomly.

The pattern of differentiated homeward orientation behaviour indicates that it results from visual perception or gender-specific motivation mechanisms and that males and females behave in a different way close to the habitat border. Increased emigration rates as a result of higher spider mobility together with the absence of visually orientation towards the patch border suggest the presence of an Allee effect in low-density patches.

Keywords: Allee effect, dispersal, field experiment, *Pardosa monticola*, sexual variation

Introduction

A key factor driving the dynamics of spatially structured populations is the ability of organisms to move between spatially separated habitat patches [Zollner & Lima 1999]. At present, behavioural mechanisms underlying such movements are poorly known, especially for non-vertebrate taxa. Many models do assume random walks, however often because of methodological simplicity rather than biological relevance [Lima & Zollner 1996]. Such mechanism may not be applicable to a large set of species for which dispersal and movement involve at least some element of decision-making [Lima & Zollner 1996]. Non-directional [i.e. diffusive] movement behaviour can be particularly costly in highly fragmented landscapes where it may prevent dispersers from locating suitable habitat for feeding and future reproduction. At the same time, extended movements across a non-suitable [i.e. 'hostile'] matrix may provoke substantial predation risk [Kisdi 2002]. One may therefore expect natural selection to favour mechanisms that increase an organisms' ability to recognize suitable habitat patches and minimise unplanned or unexpected emigration in certain stages of its life cycle [Freake 1998].

In wolf spiders and related families, cursorial dispersal reflects the most important mode of movement and dispersal [Bonte & Maelfait 2001; Kreiter & Wise 2001; Henschel 2002; Morse 2002]. It is linked to the overall pattern of high cursorial activity in this group of arthropods [Bonte *et al.* 2003c], mainly related to mate searching behaviour in males and foraging behaviour in gravid females [Baert & Maelfait 1975]. Cost of cursorial dispersal in spiders is on average low although mortality can be substantially high in populations with high dispersal rates [Morse 1997]. Cursorial activity is generally assumed to be higher in males than in females, and this pattern is believed to explain the widespread male bias in pitfall records outside optimal habitat [Bonte & Maelfait 2001]. Male-biased dispersal can be predicted when local mate competition exceeds resource competition, for instance in polygynous or promiscuous mating systems where female fitness is limited by intrinsic factors [Perrin & Mazalov 2000]. In absence of mechanisms of patch recognition and homeward orientation, high levels of cursorial mobility may increase chances of diffuse patch emigration, especially when habitat boundaries are smooth [Kuussaari *et al.* 1998]. At present there is a critical lack of empirical study on mechanisms of dispersal and orientation in invertebrates, and particularly on the link with population patterns at a landscape level.

In this study we test whether orientation behaviour in wolf spiders *Pardosa monticola* [Clerck 1757] can explain the observed male-biased dispersal across the non-suitable matrix [moss dune] and whether it can compensate emigrative diffusion due to high cursorial activity. On the moss-dune, spiders are exposed to high temperatures, a low humidity and very low or absent prey availability during summer [Provoost *et al*. 2002; Bonte, unpub. data]. Previous studies [*e.g.* Morse 2002] showed that orientation in species of this genus is mainly visual-based, although use of astronomical cues [Papi 1955; Papi & Syrjämäki 1963, both cited in Morse 2002], chemical cues [e.g. soil chemistry or herb volatile compounds] or effects of experience [Morse 2002] have been suggested. Habitat quality, reflected by grassland height and population density, is the primary factor affecting local population dynamics [Bonte *et al*. 2003c]. We hypothesise that cursorial activity is lower in high-density habitats and that this results in lower diffusion rates throughout the season.

Material and methods

Study species

The Wolf spider, *Pardosa monticola*, a widespread species in Europe and Asia, typically occurs in short and oligotrophic grasslands and heathland [Wiebes & Den Hollander 1974; Alderweireldt & Maelfait 1990]. In Flemish and Dutch coastal dunes, the species prefers grey dune grassland, grazed by rabbits and young dune slacks with a moderate vegetation coverage, where it is known to survive periods of flooding during winter [Van der Aart 1975; Maelfait *et al*. 1989; Bonte and Maelfait 2001]. Due to its regional scarcity, the species is listed on the Flemish Red List of endangered spiders [Maelfait *et al*. 1998]. During winter, *P. monticola* retreats in juvenile or subadult instars in rough, litter-rich vegetation. Males have been observed to diffuse cursorially on grey dunes with different amounts of bare sand [Bonte & Maelfait 2001]. The species is the only *Pardosa* within the habitat and, as other species from this genus, cursorial, nomadic and non-territorial [Morse 1997; Bonte & Maelfait, pers. obs.]. Because of the non-territorial behaviour, movements of individuals [e.g. males] only depend on decision-making, based on criteria as vegetation features, microclimate and mate availability and not on interspecific antagonistic reactions. Ballooning dispersal occurs rarely [Bonte *et al.* 2003d] and only during periods of food shortage in the early juvenile instars [Bonte & Maelfait 2001].

Field experiment

Fieldwork was conducted in a coastal grey dune area near Ghyvelde, France [51°03'N, 2°33'E] consisting of grassland patches with low grass and sedge sward interspersed by moss-dominated dunes [details in Provoost *et al.* 2002]. For our experiment we selected three small grassland patches [0.28 - 0.36 ha], surrounded by moss dunes and separated by pairwise distances of 243-335 m. As maximal cursorial dispersal distances of *P. monticola* on moss dunes are estimated at 150 m for males and 280 m for females [and average less than 130 m for both sexes; Bonte *et al.* 2003c], the selected grassland patches could be considered as sufficiently separated, with negligible movement interference between the patches.

We conducted standardized, bi-weekly counts between May 1st and June 14th 2000 in 30 1m^2 quadrats randomly placed in each of the three grassland patches, and analysed the counts by Generalized Linear Models with numbers of females and males as response variable [Poisson distributed] and patch, sex, and sampling period as factors. Estimated densities per patch were 0.43 ind./m^2 [further referred to as low density population L], 1.23 ind./m^2 and 1.66 ind./m^2 [further referred to as high density populations H1 and H2, respectively]. Densities differed between patches [$F_{2,888}=103.22$; $P<0.0001$] and changed over the course of the sampling period [$F_{4,888}=13.90$; $P<0.0001$] in a different way for males and females [period*sex interaction: $F_{4,888}=33.21$; $P<0.0001$]. Sex ratios, calculated as the rate of maximal male density [second half of May] over maximal female density [second decade of June] were 1.27, 1.04 and 1.09 in populations L, H1 and H2 respectively. None of these ratios significantly differed from 1 [χ^2-tests: all $P > 0.05$]. In May, average grass height in all patches was 5 cm and did not exceed moss height in the dune zone. In June, grasses were 3-5 cm taller than the surrounding moss dune in the low-density patch L and 5-20 cm taller in the two high-density patches H1 and H2.

Between 1 May and 14 July 2000, rows of three pitfall traps [diameter of 4 cm] were placed in the centre of each grassland patch ['core habitat'], at 3 m and at 10 m from the grassland edge within the moss-dominated matrix. All traps were emptied every second week. As pitfall captures reflect both levels of activity and of population density [Baert & Maelfait 1975], unbiased period specific mobility estimates [within and between grassland patches] were obtained by dividing the number of trapped males and females after each bi-weekly sampling period by their mean density in the core habitat [estimated independently, see above] at the start of the same bi-weekly sampling period. Hence, this ratio indicates the number of individuals captured relative to the patch-specific population density. In the core habitat, the value is a measure of the activity; within the matrix it represents emigration rates.

Between 14-16 May 2000 and 18-20 June 2000, a total of 72 pitfall traps [diameter of 4 cm] were placed in circular plots [radius of 70 cm and with one trap every 5 degrees] around each of four releasing points at the three patches: [i] at the centre of each patch, [ii] at the patch edge, [iii] at 1 m from the edge; and [iv] at 3 m from the edge. Experimental periods coincided with two distinct reproductive stages, i.e. mating [peaking in May] and egg production [peaking in June] [Bonte & Maelfait 2001]. All experimental individuals were collected during the morning preceding each experiment and marked with one coloured paint dot on the caudal part of the prosoma. In May, only spiders from the local patch populations were tested. Because individual distances covered within each patch are sufficiently large to induce 'edge' effects in small grassland remnants [Bonte *et al.* 2003c], we complemented these individuals by individuals from a population in a distant dune area [Westhoek Nature Reserve, 3.2 km away], which were marked with a different colour code. After marking, individuals were released in groups of 1-5 individuals at the centre of each circular plot and pitfalls were checked every 30 minutes. Trapped individuals were removed from the experiment, whereas non-trapped individuals were released in the same or another experimental plot till 30-50 individuals were captured per plot, resulting in a total of 1572 experimental individuals. For each individual, the direction of movement between points of release and of capture was recorded, with 0° as reference for the shortest possible orientation relative to the grassland patch. The same 0°-direction was retained in experiments in the core habitat and at the edge of the grassland.

Statistical analysis

Estimates of mobility [see above] approached normality after Ln-transformation. Data were analysed by Mixed Models [SAS version 8.1] with grassland patch, distance from patch edge and sex as fixed factors. Results from the orientation experiment were analysed with circular statistics [Zar 1994]. For each experiment, the mean angle [μ], angular dispersion [r], circular standard deviation and 95% confidence were calculated. Rayleigh's tests were used to test for circular uniformity [directional versus random movement]. In the case of circular uniformity, variation in orientation between sexes and populations was tested with Watson-Williams F-tests. These tests compare the lengths of the mean vectors for each sample with that for the pooled data of the two samples [Zar 1994].

Results

Variation in mobility

Levels of mobility differed significantly between grassland patches, periods and sexes, and varied significantly with distance to the grassland edge [Table III.7-1]. In the high-density patches, mobility was higher for males [6.82±2.97 captured spiders/patch population density] than for females [3.93±3.28 captured spiders/patch population density]. Only in the low-density patch, female mobility was slightly higher [27.38±2.77 captured spiders/patch population density] than those for males [22.87±5.20 captured spiders/patch population density], explaining the interaction between sex and patch. Within grassland patches, mobility was significantly higher in population L compared to the high-density patches H1 and H2, with the latter two being not significantly different [Fig. III.7-1]. Levels of mobility decreased with increasing distance to the grassland edge and were always lower in the dune matrix compared to the grassland patch [Fig. III.7-2].

Table III.7-1 - Effects of grassland patch, sex, and distance from grassland edge on levels of cursorial mobility in P. monticola. See text for details.

Factor	Num df	Den df	F	P
Patch	2	262	64.64	<0.0001
Distance	2	262	64.50	<0.0001
Sex	1	262	4.21	0.042
Patch x Distance	4	258	1.09	0.364
Patch x Sex	2	262	3.07	0.049
Distance x Sex	2	256	0.17	0.845
Patch x Distance x Sex	4	252	0.51	0.729

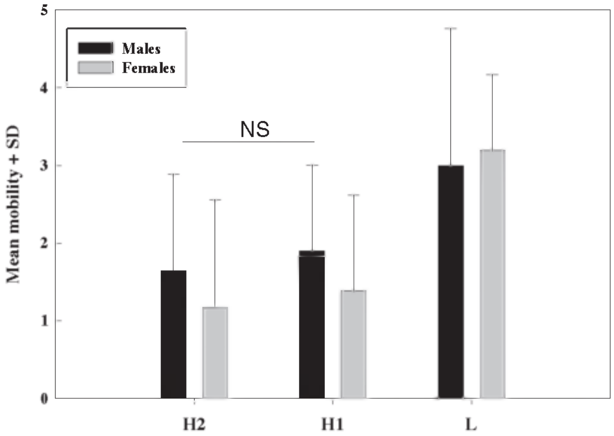

Fig. III.7-1: Levels of cursorial mobility by male and female P. monticola in three grassland patches differing in population density; L= low density, H1 and H2 = high density [see text for details].

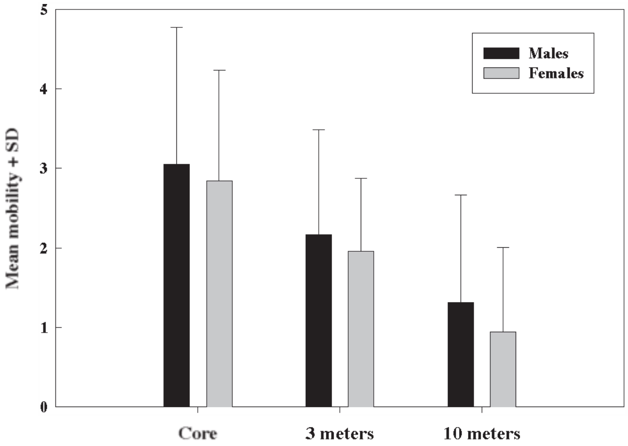

Fig. III.7-2: Levels of cursorial mobility by male and female P. monticola in the core habitat and at three and ten meters from the grassland edge in the moss matrix outside the core habitat.

Variation in homeward orientation

Results of the orientation experiments are summarised in Table III.7-2. In the first experiment [May], movement angles did not differ from a pattern expected under random movement for both males and females. In the second period [June], females from the high-density patch showed directional movement when released at the border or at 1 m from the edge, independently of reproductive status or population of origin [i.e. local versus distant] [Fig. III.7-3]. Angles of movement of these individuals did not significantly differ from 0°. In contrast, female movements were not different from random when released in the patch or at 3 m from the edge, nor for females in the low-density patch [all locations] and for males in both high- and low-density patches [all locations]. Furthermore, in locations where directional movement was observed [i.e. at grassland edge and at 1 m distance], mean directions of movement did not differ between females with or without egg sacs [edge: $F_{1,77}$=0.002; 1 m: $F_{1,78}$ =0.67; all $P > 0.05$]. Likewise, no differences occurred between local and non-local individuals [edge: $F_{1,76}$= 0.66; 1 m: $F_{1,81}$=0.002; NS].

Fig. III.7-3: Histograms depicting the results of orientation experiments for male and female P. monticola released at different distances from grassland patches: [a-b] at grassland centre; [c-d] at grassland edge; [e-f]: at 1 m from edge; [g-h]: at 3 m from edge]; left panels: males, right panels: females.

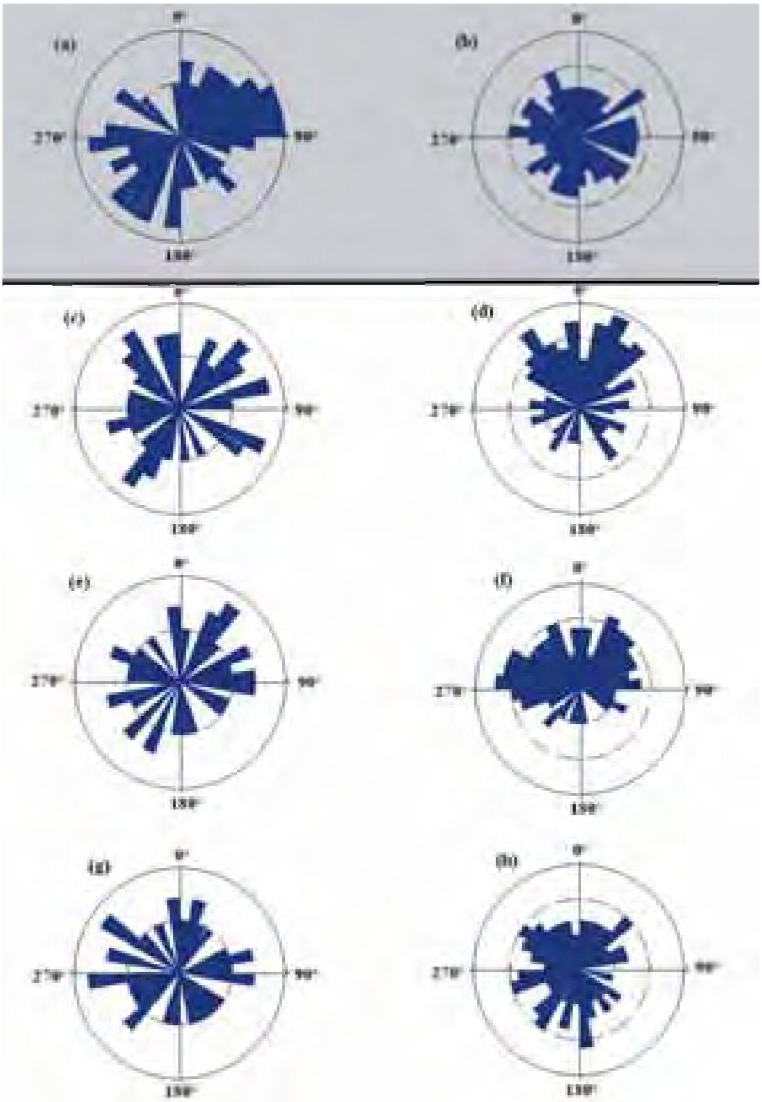

Table III.7-2 - Effects of period, location, sex, reproductive status, and population of origin on the level of homeward orientation in P. monticola. n = number of individuals; μ = mean angle of movement [with 95% confidence intervals in case of directional movement]; r = angular dispersion; Rayleigh test for directional movement, * $P<0.05$; ** $P<0.01$; Fem – eggs = females without eggsacs; Fem +eggs = females with eggsacs; native = individuals from local population; foreign = individuals from distant population. See text for details.

Patch	**Period**	**Sex –reproductive status [population]**	**Circle**	**N**	**μ [95% conf. int.]**	**r**
High density	May	Males [native]	Patch	43	348.63°	0.14
			Border	50	137.81°	0.17
			1meter	74	323.83°	0.10
			3 meter	47	351.06°	0.16
		Fem -eggs [native]	Patch	49	277.12°	0.13
			Border	57	356.40°	0.19
			1meter	57	346.31°	0.20
			3 meter	33	305.38°	0.04
	June	Males [native]	Patch	38	89.81°	0.13
			Border	19	46.70°	0.24
			1meter	16	16.39°	0.37
			3 meter	20	294.82°	0.18
		Fem -eggs [native]	Patch	24	233.10°	0.05
			Border	22	13.80° [21.96°]	0.66**
			1meter	24	340.01° [38.83°]	0.39*
			3 meter	21	267.57°	0.08
		Fem +eggs [native]	Patch	20	271.54°	0.18
			Border	22	12.66° [40.83°]	0.40*
			1meter	28	326.50° [39.01°]	0.37*
			3 meter	20	298.56°	0.14
		Males [foreign]	Patch	20	244.03°	0.25
			Border	23	287.94°	0.14
			1meter	18	175.13°	0.12
			3 meter	15	2.96°	0.07
		Fem -eggs [foreign]	Patch	16	70.71°	0.14
			Border	18	359.46° [38.03°]	0.46*
			1meter	17	358.00° [34.22°]	0.53*
			3 meter	14	261.00°	0.34
		Fem +eggs [foreign]	Patch	21	70.47°	0.15
			Border	17	359.33° [37.67°]	0.48*
			1meter	17	11.79° [39.21°]	0.45*
			3 meter	17	284.28°	0.18

Patch	Period	Sex –reproductive status [population]	Circle	N	◀ [95% conf. int.]	r
Low density	May	Males [native]	Patch	50	137.44°	0.16
			Border	50	22.13°	0.13
			1meter	44	167.56°	0.09
			3 meter	46	278.66°	0.18
		Fem -eggs [native]	Patch	34	213.12°	0.19
			Border	37	67.09°	0.09
			1meter	43	110.56°	0.18
			3 meter	34	202.78°	0.14
	June	Males [native]	Patch	40	23.23°	0.16
			Border	30	321.71°	0.11
			1meter	29	117.09°	0.22
			3 meter	18	216.17°	0.19
		Fem -eggs [native]	Patch	33	23.50°	0.09
			Border	23	59.37°	0.16
			1meter	29	138.12°	0.20
			3 meter	31	229.75°	0.11
		Fem +eggs [native]	Patch	34	67.81°	0.21
			Border	22	276.74°	0.08
			1meter	18	310.45°	0.15
			3 meter	30	58.08°	0.19

Discussion

To estimate rates of cursorial activity in core habitat and diffuse emigration at habitat edges, we combined traditional density estimates with experimental capture-recapture data. Our results confirm the hypothesis that increased cursorial activity in low-density habitat, characterised by low vegetation height and hence poor quality [Bonte *et al.* 2003c], results in increased emigration rates by *P. monticola*. As is generally the case in natural populations, patch quality and population density covary. Hence, without a more complex experimental design we cannot discriminate between both effects. Diffusive emigration rates were highest close to the patch border, while both emigration and cursorial activity in core habitat was higher in the low-density population. Both rates further showed substantial temporal variation. We did not find evidence for homeward orientation by males and females during May, when grassland height approached that of the moss dune matrix. In June, no homeward orientation was observed in the low-density patch. In the high-density patch, however, females but not males showed evidence of homeward orientation close to the grassland-moss dune ecotone. At distances of three meters from the grassland edges, however, females too showed random movements. The observed pattern of homeward orientation suggests that it results from visual perception with males and females differing in perception ability or from sex-specific motivations towards the core habitat.

Increased cursorial activity in arthropods inhabiting low quality habitat was previously demonstrated by Kindvall *et al.* [1998] [cricket] and Kreiter & Wise [2001] [spider], and assumed to be an adaptation to low mate-location probabilities under low population density [Kindvall *et al.* 1998], or to reflect conditions of food restriction [Kreiter & Wise 2001]. In populations with highly contrasting boundaries, increased levels of cursorial activity do not enhance the risk of leaving a preferred habitat patch, although energetic costs can be high [Morse 1997]. In open habitats that are smoothly connected to non-suitable matrices, however, increased levels of mobility may lead to higher emigration rates, hence increasing the risk of Allee effects in low density populations [Kuussaari *et al.* 1998; Thomas & Kunin 1999]. In our study, emigration across the moss dune matrix is additionally assumed to increase mortality because of the absence of prey and lethal microclimatological conditions in this matrix [Bonte *et al.* 2002e].

Results from our experiment confirm earlier findings that dispersal in *P. monticola* is generally male-biased [Bonte & Maelfait 2001]. Even in absence of male-biases in sex ratios, local competition for mates [Perrin & Mazalov 2000] may cause such dispersal pattern given that male *P. monticola* perform multiple mating under laboratory conditions [Bonte & Maelfait, unpub. data]. As genetic diversity in this species is not lower in low quality patches [Bonte *et al.* 2003c], inbreeding avoidance [*sensu* Perrin & Mazalov 1999; Perrin & Mazalov 2000] may probably not trigger the higher dispersal rates in low-density habitat. Under low population density, cursorial activity by female *P. monticola* exceeded that by males, as indicated by the sex*patch interaction. During late spring and early summer, when prey availability is critical for reproduction [Kreiter & Wise 2001], prey abundance decreases substantially in grey dunes with poor soil development and low vegetation height, but not in grasslands with a well-developed organic soil layer [Bonte *et al*. 2002e]. Increased mobility and emigration rates in the former hence suggests that resource competition [Perrin & Mazalov 2000] may trigger the observed bias towards female dispersal during that period. Higher emigration rates resulting from increased mate location probably only hold for adult males since their activity, but not that of females, is strongly related to mate seeking [Maelfait & Baert 1975]. Female activity is mainly related to the deposition and incubation of egg sacs and to feeding activity for egg production [Maelfait & Baert 1975], and as such, increased activity may result from increased searching for optimal habitat [Humphreys 1987]. In the low-density patch, vegetation structure is less complex and can possibly result in fewer optimal microhabitats for egg incubation as spiders have fewer opportunities to orientate themselves on the vegetation in an ideal position towards the changing inclination of sun radiation.

Poor homeward orientation behaviour by females may increase the probability of patch emigration, in particular if patch boundaries are smooth due to small vegetation differences with the surrounding matrix. As shown by our experiments, *P. monticola* females showed homeward orientation close to the border of the high-density patch in a period when grassland height substantially exceeded that of the matrix, suggesting the use of visual cues over short distances. However, chemical cues from vegetation or soil cannot a priori be, and would be a valid alternative if full-grown herbs produce olfactory cues different from those of low, fresh herbs and mosses. Contrary to earlier findings by Morse [2002] familiarity with the area, did not affect the ability of homeward orientation in our study, although we can assume that individuals often experience excursions outside the core habitat, necessary for the stimulation of homing behaviour [Conradt *et al.* 2000; Conradt *et al*. 2001].

The observed difference in orientation behaviour between sexes may have resulted from different perception abilities towards structural contrast at the habitat boundary, from different levels of motivation, or from both.

Differential response by males and females to habitat cues [resource availability for males and females, structural contrasts at habitat boundary] and social cues [competing males, male harassment to females] may cause different orientation behaviour between the sexes. Since adult male activity is mainly related to mate location and less so to foraging, males but not females may succeed in continuing mate seeking behaviour across the matrix, and by doing so, increase their chances of reaching other populations in the neighbourhood. Costs of diffusive emigration in a heavily fragmented landscape may, indeed, be very high for gravid females due to a strong dependence on food for egg production and suitable microclimatological conditions for successful egg development [Humphreys 1987]. Social cues seem to be of minor importance since avoidance of competition by leaving the patch certainly decreases mating chances due to low densities of females.

Although we believe that stress caused by handling individuals was restricted [such as in comparable mark-recapture studies; Morse [1997]], sex-related escape behaviour [*e.g.* males randomly fleeing while females searching higher vegetation to hide if released close to the patch border] cannot be excluded. Artificial or natural predation risk hence provides an alternative explanation for the observed orientation behaviour, yet does not change the biological interpretation of the observed patterns: females return to the patch in search for optimal resources [prey availability, microclimatological conditions or shelter against predators], while males keep moving in a random way, thus restricting their chances to return to the grassland patch of origin but increasing the probability of gene flow between closely located populations.

The above results suggest that increased levels of cursorial activity within patches may lead to increased levels of emigration rates when not counteracted by behavioural cues such as homeward orientation, and more generally, that behavioural mechanisms may restrain or enhance population dynamics. In the case of low population densities, high emigration rates combined with absence of visual orientation may increase the risk of Allee effects [Courchamp *et al*. 1999; Stephens & Sutherland 1999]. At the same time, however, increased cursorial activities within patches may counteract such Allee effects by increasing chances of local mating [Kindvall *et al*.

1998]. The latter may have been the case in the low-density grassland patch in our study area, where no reduction or delay of reproduction was observed [Bonte, unpub. data].

Interactions between individual-level behaviour and population-level dynamics, such as discussed in this paper, are much more complex than those usually incorporated in individual-based population models. At least in some cases, incorporation of behavioural mechanisms, such as variability in mobility behaviour in relation to distances from habitat edges, may substantially increase the biological relevance of these populations models. It also stresses the need for further research on the behavioural ecology of ecological landscapes [*sensu* Lima & Zollner 1996; Boudjemadi *et al*. 1999]. The latter may be particularly relevant in the case of endangered species, where integration of behavioural components with population dynamics may result in a better comprehension of the species life history, and hence, the implementation of more realistic conservation strategies [Sutherland 1998].

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III.8

Spider dispersal in fragmented coastal grey dunes: general discussion

FOTO: DRIES BONTE

Overview of the main results

Spider species, characterised by a high degree of habitat specialisation, have lower ballooning propensities than species occurring in a wide variety of habitats. This pattern depends additionally on phylogenetical background: species belonging to the *orbicularia* have better developed dispersal propensities than those belonging to the *RTA*-clades. Hence, ballooning dispersal appears to be better evolved in more sedentary, in general small web-building species than in larger active hunters, which have a restricted time window for aerial dispersal and do not use silk for prey capture. The applied measure of dispersal, together with the interaction between patch connectivity and patch area explain distribution patterns within grey dune fragments. Niche breadth did not contribute to the observed distribution patterns. This importance of dispersal in shaping species distribution affects our perception of species' fundamental niches and indicates that both source-sink and metapopulation mechanisms have an important impact on distribution patterns.

Our experiments on variation of ballooning latency in *Erigone atra* indicate that proximate [acute food deprivation], ontogenetic [feeding and temperature conditions during the juvenile development] and possibly genetic factors influence individual latencies to perform pre-ballooning tiptoe-behaviour. Because repeatability is high at short intervals of 1 h but low at longer intervals of a week or more, feeding history during the adult life-stage or age also determines the individual propensity to perform ballooning dispersal.

The spatial distribution of *Pardosa monticola* is primarily related to patch quality, which was determined by patch size and vegetation height. Patch connectivity, as estimated for ballooning dispersal contributed significantly, but less to the observed distribution pattern. The probability of short time colonisation increased with high patch quality and high levels of cursorial connectivity, whereas local extinctions appeared to be mainly stochastic. The population of *P. monticola* can therefore de defined as a habitat-quality-dependant metapopulation. This observation of limited dispersal abilities contradicts with the findings of a low genetic differentiation [as revealed by allozyme electrophoresis] and stresses the importance of both direct and indirect estimates of dispersal in the interpretation of population-genetic patters.

As in *Erigone atra*, acute food deprivation is the most important trigger to stimulate the performance of tiptoe-behaviour in *P. monticola*. By using this species as a model, we demonstrated for the first time regional and interdemic variation in ballooning propensity. Geographic variation appears to be determined by the degree of patch isolation within the dune landscape and is assumed to be selected against in strongly isolated populations. As maternal condition and fitness also decrease with increasing patch isolation, selection against dispersal may enhance a mechanism of risk spreading. Interdemic variation exists between populations of the Flemish coastal dunes. The occurrence of tiptoeing offspring within maternal clutches is highest if maternal fitness is low, while the frequency of potential ballooners within clutches was higher in habitats where prey occurrence is guarantied [predictable habitats: dune slacks] than is habitats where prey deprivation is possible during dry summer period [unpredictable dune grasslands]. However, the genetic basis of ballooning dispersal remains unclear, but, even if only maternal effects are responsible for the observed variation, it appears to be the most adaptive response since it enables individuals to use information of the environment more completely. This results in optimal dispersal strategies in function of habitat configuration, quality and predictability.

In contrast to aerial dispersal, cursorial dispersal is the most important dispersal mode for adult *P. monticola*. In a grassland-moss dune landscape, grassland is the core habitat while moss-dominated vegetation is only occupied after diffusive dispersal out of the core habitat. Patch-emigration is higher in grasslands of low quality, where densities are low, than in high quality grasslands where *P. monticola* occurs in higher densities. This patterns results from higher mobility rates in the low-density habitat [presumably because of low population sizes and hence lower mate encounter rates and a scarcer prey presence] and is strengthened by the absence of female orientation towards the core habitat after diffusive patch emigration into the matrix. The observed pattern of homeward orientation suggests that it results from visual perception with males and females differing in perception ability or from sex-specific motivations towards the core habitat.

General discussion

Interspecific variation and species distribution

As pointed out by Weyman *et al.* [2002], interspecific variation in ballooning propensity has mainly been linked to mechanisms related to habitat stability and predictability, not to the least because of the dominant observations of ballooning species from arable land. Our data support the hypothesis of Parvinen [1999] and Mathias *et al.* [2001] that dispersal is selected against in heterogeneous landscapes, in which costs of reaching suitable habitat are high. These costs are especially high for specialised species and result into a covariation between dispersal and the degree of habitat specialisation [or realised niche breadth]. As predicted by theoretical models [Kisdi 2002], dispersal propensity in spiders from grey dunes is selected as risk spreading in generalist species, while it is selected against in specialist species. Selection for dispersal in generalists should as a result favour risk spreading because of a suboptimal adaptation to the local habitat, while dispersal is selected against in specialists by a strong adaptation to local environmental conditions.

A well-developed dispersal capacity is the first condition for a successful colonisation [e.g. Den Boer 1970; Thomas *et al.* 2001b; Bullock *et al.* 2002] and is shown to be related to local distribution in some insect families [Malmqvist 2000] or patch occupancy in fragmented habitats [Hanski 1999a]. However, dispersal interplays with niche breadth and landscape configuration [Pulliam 2000] in shaping species distribution patterns, especially in explaining the presence of species in sink habitats. Habitat fragmentation may both promote and reduce mobility, depending on the degree of resource or habitat specialisation [Wiens 2001]. Thus, ecologically related species occupying the same environment may differ markedly in their responses to landscape change and fragmentation, depending on how dispersal and niche breadth are expressed in their respective populations, possibly as a result of local adaptation.

Our data, however, do not show a relationship between level of habitat specialisation and species distribution, which would be expected if specialist spiders were more sensitive to changes in habitat quality, as shown for dragonflies in Central-Finland [Korkeamäki & Suhonen 2002]. It does neither explain patterns in species distribution in interaction with connectivity, which would indicate different sensitivities to patch isolation for specialist and generalist species. Such a relationship would be expected if generalist species survived better in other habitat types in the matrix. Only the landscape configuration [patch isolation and connectivity] and ballooning propensity, a measure of dispersal potential, explained distribution patterns. As a result, specialised [hence intrinsically rare] species can be predicted to become rarer if fragmentation increases and connectivity decreases.

Dispersal and population dynamics in a dune wolf spider

Cursorial and aerial dispersal, influenced population dynamics of *Pardosa monticola* at different time scales and ballooning seems especially important in structuring population at longer time intervals, as observed for species distribution patterns in general. Because habitat quality is the best predictor of occupancy and colonisation patterns, the metapopulation structure of *P. monticola* in coastal dunes primarily depends on habitat quality, as is the case for source-sink dynamics. The low level of genetic diversity in *P. monticola* was in concordance with patterns observed in other dune dwelling arthropods [Ramirez & Froehlig 1997; Boulton *et al.* 1998], suggesting similar environmental selection pressures. The estimated low genetic differentiation did not complement the estimated dispersal and the spatial distributional pattern of *P. monticola* in the study area, as suggested by Whitlock & McCauley [1999]. This discrepancy between genetic and distributional data may have different reasons, as reported in chapter III.5, but confirms the need for both direct and indirect estimates of dispersal when aiming to interpret current patterns of genetic differentiation [see also Peterson *et al.* 2001].

Sources of variation in spider dispersal

The significant interspecific variation in ballooning propensity indicates that this dispersal mode co-evolved with morphological traits and characteristics related to the degree of niche specialisation. Because observations were made on spiders from the Flemish coastal dunes, variation due to different regional selection pressures was eliminated, and interspecific variation could only be attributed to evolutionary mechanisms.

As suggested by Massot & Clobert [2000], variation in the dispersal-linked tiptoe behaviour is determined by *innate* [prenatal] and *proximate* postnatal factors. In *Erigone atra,* the interaction between diet and temperature was significant and indicates a complex reaction of spiders to different postnatal environmental factors. The strong effect of temperature during rearing on ballooning latency may be an inherent physiological response, as found by Dingle [1968] in *Oncopeltus*. The finding that different nutritional conditions during juvenile development induced different behavioural ballooning patterns was expected, and stresses the importance of resource availability as a dispersal trigger. The direction of the species' reaction towards feeding stress contradicts however with the findings of Legel & Van Wingerden [1980], and suggests that different species or populations are able to respond in different ways to changing environmental conditions. Nevertheless, our data show that ballooning latency is influenced by physiological responses to environmental circumstances during juvenile development. Mothers therefore influence the ballooning initiation of their offspring by selecting environments of varying quality for egg deposition.

Family effects explained considerable phenotypic variation, but were not statistically significant, because only 13 families were included in the quantitative study and the overall high amount of residual variation in the expression of behaviour [Chris Boake, pers. communication]. However, it stresses the importance and interaction of genetic components in the expression of behavioural traits, narrowly linked to dispersal. This low genotypic variation is concordant with overall low heritabilities for behavioural traits [Roff & Mousseau 1987; Hoffmann 1999] and indicates that environment and genotype sum and interact in the expression of this dispersal-linked behavioural trait. Although no effects of the maternal condition on offspring ballooning latency were found, we cannot conclude that genetic variation has to be additive, since *e.g.* egg quality [Diss *et al*. 1996; De Fraipont *et al*. 2000] can have a direct effect on the offspring behaviour, resulting in similar dispersal patterns among offspring from one family. The detection of the genetic source of variation [additive versus non-additive] in ballooning dispersal needs hence further research. As the additive component of ballooning behaviour was high in the spider mite *Tetranychus urticae* [Li & Margolies 1993; 1994], a similar magnitude can be expected in related Araneae. In contrast to experiments with this phytophagic arthropod, in which rearing conditions and especially food quality can be more easily controlled, minimising the residual variance in spider ballooning latency seems necessary and a challenge in the study of the evolution of ballooning dispersal.

Because studies of intraspecific geographical differences offer best hope for dissecting the causes of behavioural evolution [Arnold 1992; Foster 1999; Riechert 1999] we conducted common garden experiments on *Pardosa monticola* offspring, reared from collected mothers out of different populations. Interdemic and geographic variation in ballooning propensity of *Pardosa monticola* illustrated the existence of two possible sources of variation. The relationship between interdemic variation in ballooning performance and the environment revealed the possibility of natural selection on the ballooning dispersal or on mothers, which trigger [or reduce] ballooning dispersal behaviour in their offspring. Female *P. monticola* from strongly isolated populations, have a low proportion of [potential] ballooning offspring and presumably increase in this way their fitness by minimising dispersal mortality. In contrast, high dispersal rates in the open landscape can reduce inbreeding [Chesser & Ryman 1986; Crespy & Taylor 1990; Perrin & Mazalov 1999] and kin competition [Hamilton & May 1977; Perrin & Lehman 2001; Lehman & Perrin 2002]. Because clutch size is largest in this large population, the overall low number of fast reacting potential ballooners within each clutch can be selected in function of risk spreading [Kisdi 2002]. Similarly, the large variation within mothers can result from selection on risk spreading within the population. As a result, not selection for, but selection against dispersal augments the species' fitness in isolated populations and potentially acts asymmetrically and directionally on offspring ballooning propensity, independently of whether it is locally influenced by mothers. Alternatively, selection may directly act on the dispersal behaviour, but, as both the frequency of ballooning offspring within the clutches and the frequency of females with [at least one] ballooning offspring show the similar predicted differentiation in function of the habitat configuration, an adaptive value is almost certainly present. We can, however, not distinguish whether selection acts directly or indirectly, via maternal effects, on the dispersal behaviour of the wolf spider offspring.

As the presence of ballooning individuals within clutches from the half-open landscape is related to the maternal condition, we can conclude that the observed interdemic pattern at this spatial scale most likely results from interaction with maternal, non-additive variation over subsequent generations. As in *Erigone atra,* we did not find similar maternal condition effects for tiptoe frequency, possibly because of constraints in observation time or because of the presence of other maternal effects, influenced by the maternal physiology [egg quality: lipids, proteins].

Nevertheless, although we are not able to distinguish unambiguously between additive and non-additive variation in offspring ballooning propensity, we demonstrate for the first time geographic and interdemic variation within this behavioural trait. The existence of geographic variation in spider behaviour has until now only been demonstrated for male courtship behaviour in the wolf spider *Schizocosa crassipes* [Miller *et al*. 1998] and in diet breadth, conspecific agonistic behaviour, territory size and antipredator retreat probability in the funnel-web spider *Agelenopsis aperta* [Foster 1999]. In the latter, spiders from large populations were even behaviourally adapted to local conditions, but gene flow between environments constrained the behavioural adaptation in small patches [Riechert, 1993a,b].

Besides aerial dispersal, or at least the propensity of the preballooning behaviour, cursorial dispersal rates also show considerably variation between [sub]populations, inhabiting grey dune patches of different quality.

Our results confirm the hypothesis that increased cursorial activity in low-density habitat, characterised by low vegetation height and hence poor quality, results in increased emigration rates by *P. monticola*. As is generally the case in natural populations, patch quality and population density covary. Hence, without a more complex experimental design we were not able to discriminate between both effects. A similar increased cursorial activity in arthropods inhabiting low quality habitat was previously demonstrated by Kindvall *et al.* [1998] and Kreiter & Wise [2001], and is assumed to be an adaptation to low mate-location probabilities under low population densities [Kindvall *et al.* 1998], or to reflect conditions of food restriction [Kreiter & Wise 2001]. Therefore, increased mobility and emigration rates in the low quality population suggest that resource competition [Perrin & Mazalov 2000], especially prey shortage and the lack of incubation sites, triggers the observed bias towards female dispersal during that period. Higher emigration rates resulting from increased mate location probably hold for adult males only since their activity, but not that of females, is strongly related to mate seeking [Maelfait & Baert 1975]. Also, in contrast to females living in and around grey dune patches of high quality, females from low-quality patches are not able to perform homeward orientation, because of the presence of smooth edges. Since emigration rates are already higher in the latter, an Allee effects may occur [Kuussaari *et al.* 1998; Thomas & Kunin 1999] because of increased emigration rates in low-density populations. At the same time, however, increased cursorial activities within patches may counteract such Allee effects by increasing chances of local mating [Kindvall *et al.* 1998], as may have been the case in the low-density grassland patch.

Conclusions

Aerial dispersal, here estimated by investigating the propensity of ballooning, in spiders from fragmented grey dunes appears to be selected against if chances of reaching suitable habitat are low. Ballooning is hence restricted in strongly isolated populations or in species with a high degree of specialisation to the grey dune habitat. In other words, if the landscape becomes more and more heterogeneous, dispersal is selected against [Matthias *et al.* 2001].

According to Desender [1987], the change in frequency of dispersers [in carabid beetles] within populations does not result from natural selection but from *directional gene-migration*. This semantic debate originates from the question whether fitness of non-dispersers increases in isolated, older or stable populations. The latter argues for the mechanism of gene-migration because, in carabid beetles, not all non-dispersers had a higher fecundity or a longer life span. Experimental counter evidence was even available for many species. In spiders, in which dispersal is more passive, we believe however that this directional gene-migration, the loss of alleles coding for dispersal behaviour, is a result of natural selection. In individuals from isolated populations, fitness of residents will not be higher than those of the potential dispersers, but the cost of landing in unsuitable environments will certainly decrease the fitness of dispersers as a result of direct mortality or a possible reduced fecundity in case individuals disperse into less suitable but non-hostile habitat. Selection will, in my opinion, not increase the frequency of dispersal-alleles within a population but act against dispersing individuals because of high mortality costs in isolated populations. Not directional gene-migration but the loss of alleles coding for dispersal, as the result of natural selection against dispersal should hence be the dominant mechanism. Residents in strongly isolated populations will as a result be better adapted to the local environment because of the loss of dispersal propensity. This change in allele frequency influences hence local behavioural adaptation.

Proximate environmental factors are certainly an important trigger of spider dispersal, both for ballooning [acute food deprivation, temperature and feeding stress during the juvenile development, maternal habitat quality, landscape configuration] and cursorial dispersal [habitat quality, boundary structure]. Residual variation remains however high, as shown for ballooning propensity in *Erigone atra* and aerial and cursorial dispersal in *Pardosa monticola*. This variable dispersal propensity within offspring is consistent with the mixed Evolutionary Stable Strategy of Parker & Stuart [1976], in which each individual from a genetical monomorphic population selects a variable strategy from a common probability distribution, with the possibility of fine adjustment according to environmental conditions, in our case also maternal conditions. This apparently “random” strategy may however be a cryptic environmental or evolutionary trigger that only appears to be random because of hardly detectable relationships with the [maternal] environment. A similar and apparent randomness [or better: unexplained residual variation] has also been observed in other studies [Samu *et al* 1996; Morse 1997]. This random switching mechanism is according to Weyman *et al*. [2002] responsible for the observed variation in ballooning within populations. Although not studied in detail, the window of dispersal is different between species and within species, as dispersal is restricted to certain life stages, with different temporal distributions. Individuals hence experience different meteorological and environmental conditions and probably have different threshold values towards the important environmental stimuli. This large variation within the dispersal window is in my opinion, one of the main determinants of the large amount of unexplained variation in dispersal propensity. Additionally, the maternal habitat choice strongly influences natal dispersal. This type of condition-independent maternal effect comprises dispersal induced by the maternal choice of the habitat where offspring will hatch. This effect will even be more complex in wolf spiders, as females carry their offspring on their back for a period of 3-7 days [Bonte, unpub. data]. Natal dispersal can as a result occur if spiderlings leave the maternal abdomen at different periods. As offspring-carrying spiders remain cursorially active, maternal displacement together with the asynchronous “loss” of offspring will initially determine spiderling distribution [and hence natal dispersal] within the habitat. Although no concrete data are available, the timing of spiderlings to leave the back of their mother may also be influenced by innate and proximate factors, dependent on other selective mechanisms than described for aerial and cursorial dispersal. It is for instance not impossible that the rate of “dropping from the maternal abdomen” will depend on the clutch size in order to avoid kin competition. As aerial dispersal in wolf spiders is restricted to a small proportion of the population, mainly under conditions of food deprivation, this mode of natal dispersal [maybe we can propose the term *hitchhike-dispersal*...] can influence the local distribution of offspring within the habitat in a more pronounced way than ballooning or early cursorial dispersal.

In contrast to the apparently large residual and patch-specific variation in dispersal propensity, our general models, based upon random directional dispersal and patch-independent dispersal frequencies, predict the importance of dispersal characteristics for species distribution and population dynamics in a significant way. Interdemic variation in dispersal is hence biologically important in shaping dispersal behaviour at the individual level [within habitat distribution], but presumably of minor importance at the scale of the community. Probably, even if only a small proportion of the population is capable of successful dispersal, the absolute number of dispersers will be sufficiently high to influence population dynamics, because of the large population sizes.

However, interactions between individual-level behaviour and population-level dynamics, such as discussed throughout this thesis, are much more complex than those usually incorporated in individual-based population models. At least in some cases, incorporation of behavioural mechanisms, such as variability in mobility behaviour in relation to distances from habitat edges, may substantially increase the biological relevance of these population models. The inclusion of data on niche breadth may even elucidate species distributions, apparently not influenced by dispersal characteristics. Finally, our results stress the need for further research on the link between behavioural ecology of ecological landscapes [*sensu* Lima & Zollner 1996; Boudjemadi *et al*. 1999]. The latter may be particularly relevant in the case of endangered species, where integration of behavioural components with population dynamics may result in a better comprehension of the species life history, and hence, the implementation of more realistic conservation strategies [Sutherland 1998].

IV.1 CONSIDERATIONS FOR NATURE CONSERVATION AND FUTURE RESEARCH

FOTO: DRIES BONTE

Introduction

Grey dune, known as “Fixed coastal dunes with herbaceous vegetation” in the CORINE biotope classification [Natura 2000], is considered priority habitat in the annex I of the EU Habitat Directive [Hopkins and Radley 1998]. This status implies that grey dunes deserve special conservation attention [Herrier & Killemaes 1998b].

Coastal ‘grey dune’ is most readily defined using plant communities. Vegetation includes Atlantic moss dominated dunes as well as dune grassland [with a distinct organic soil layer] belonging to the *Cladonio-Koelerietalia* in case of lime rich grey dune and to the *Trifolio-Festucetalia ovinae* in case of decalcified grey dunes [Provoost *et al.* 2002]. Ecologically it is merely the dry component of the “stressed dune landscape”, where ecological dynamics are situated in the field of tension between top down regulating stress factors and bottom up [xerosere] organisation. The main differentiating processes are related to dune fixation, soil formation and vegetation development [Provoost & Hoffmann 1996; Aggenbach & Jalink 1999]. Variation in nutrient availability and sand overblowing result in variation of dynamics and ecosystem stability, which are believed to be related to biodiversity [Pianka 1994; Schwartz *et al.* 2000]. The relation between both is however unclear and certainly not causative in the inverse way.

Due to urbanisation and rough grass- and scrub encroachment, the grey dune area along the Western part of the Flemish coast decreased from 730 to 350 ha since the fifties. At this moment, grey dune fragments are patchy distributed within a matrix of dense dune vegetation [shrubs, dense grassland]. In comparison to other coastal dune habitats, grey dunes are characterised by a specific and endangered entomo- and arachnofauna [Bonte *et al.* 2002d]. By removing shrubs and introducing domestic grazers, local nature managers aim to restore grey dune habitat within the stressed dune landscape.

There is a general consensus that spiders are good candidates for bio-indication in terrestrial ecosystems of the temperate regions, both at the level of the population and the community or assemblage [Marc *et al.* 1999; Maelfait *et al.*, in press] and meet the criteria of *Ecological indicators* according to Dale & Beyeler [2001]. The growth rate or reproductive rate observed in natural populations can be correlated with the amount of prey ingested in the field and give an indirect estimation of habitat quality. Due to the close correspondence between vegetation architecture and the composition of the associated spider assemblage, Marc *et al.* [1999] argued that fluctuations in the spider assemblage allows bioevaluation of human disturbance. Moreover, if faunistical and biogeographical information is available, the completeness of particular areas [dependent on the scale of interest: habitat type, nature reserve, landscape] can be evaluated in function of human interference [Maelfait *et al.*, in press]. At longer-term intervals surveys by using spiders as bio-indicators may be repeated in order to assess to which extent results from nature management or restoration deviate from a predetermined norm [Goldsmith 1991].

Conservation of dune habitats

Coastal dune management aims for restoring and conserving dune-specific habitats. In contrast to higher plants and terrestrial molluscs, stenotopic arthropods from coastal and inland dune regions of Flanders [i.e. species from coastal dunes and oligotrophic grasslands] are restricted to the *stressed* and *dynamic* dune landscape [Provoost & Bonte, in press[a]]. These habitats can only be maintained under sufficient aeolic dynamics and grazing stress. Since patterns of spider distribution correspond well with patterns of other invertebrates [Provoost & Bonte, in press[b]], we will treat them as an *umbrella*-group [Simberloff 1998] for coastal dune arthropods in general, although further testing is necessary on the generality of this approach. For example, Empidid flies [*Empididae]* do not follow this pattern [Grootaert & Pollet, in press], but this may be a theoretical artefact because this family mainly radiated in humid habitats, in contrast to *e.g.* robberflies [*Asilidae]*, which are especially adapted to dry habitats [Bonte *et al.* 2002c]. Because these taxa have not evolved in all habitat types, they are as a single taxon not suitable for bio-indication in complex ecosystems.

Variation within and between patches is responsible for a high regional diversity since the spider assemblage composition of grey dunes is primarily influenced by sand dynamics and the coverage of bare sand [certainly in the dunes along the Northern-French and the Belgian coast, but less in those from the Netherlands]. Additionally, internal variation in vegetation structure and composition, especially the presence of litter-rich patches, is necessary for many spider species, apparently restricted to grey dunes. At least some of them [but this is probably a more general pattern] show shifts in habitat use during their life cycle and spend their juvenile development in litter rich vegetation [Bonte *et al.* 2000a]. Because sampling mostly occurs with pitfall traps [which mainly capture adult individuals], this multi-habitat use is presumably overlooked in many species.

Restoration of aeolic dynamics appears to be critical for the conservation of the threatened insect and spider fauna in the coastal dune region. Although theoretically simple, this measure certainly involves practical problems because it conflicts with needs for coastal defence and urban planning. At this moment, removal of aeolic barriers, such as streets and camping sites, between large dune massifs seems the best possible solution. At longer periods, however, aeolic dynamics will disappear deterministically because net-sand supply from the beach towards the dune is decreasing due to urbanisation and mechanical cleaning of beaches, which constrain the formation of new embryonic dunes.

Besides the restoration of sand dynamics, extensive grazing in combination with large-scale removal of shrubs seems to be the best management strategy to create suitable habitat for the xerotherm spider fauna. Additionally, patches will get better connected, allowing the existence and maintenance of metapopulations of spiders and invertebrates in general [see later]. Probably, vegetation dynamics under grazing management fits into a *shifting mosaic* pattern of [sub]climax vegetation as described by Olff *et al.* [1999] for woodlands. The introduction of larger [domestic] grazers will enhance the enlargement and connectivity of grassland patches, with conservation of sufficient internal structural variation and habitat variation within the entire dune landscape. Depending on the grazing intensity [mainly grazer density], the mosaic landscape will balance somewhere between a closed shrub and an open grassland-dominated landscape. Although the latter seems to be ideal for the conservation of the typical arthropod fauna, we should bear in mind that, besides the fact that many species use different habitats within their life cycle, some species are exclusively bound to sea buckthorn *Hippophae rhamnoides* and, in this way, are restricted to the coastal region [the aphid *Psylla hippophaës*, the louce *Capitophorus hippophaës*, the moth *Gelechia hippophaëla*, the mite *Aceria hippophaena,* the bore-fly *Rhagoletis batava* and the fungus *Phellines hippohaëcola*]. Especially litter-rich vegetation will disappear under high grazing intensity, and hence decrease possibilities of juvenile development for –at least some- dune arthropods. Also, high trampling will accompany a high grazing intensity and will hence decrease the presence of sufficient habitat for burrowing spiders and insects [ants]. A recent study [Lehouck 2002] focused especially on the latter because of the typical arthropod fauna, associated with ant nests.

Landscape configuration

According to our findings, conservation of specific dune arthropods should focus on the creation of large surfaces of grey dunes because species distribution and species richness of these species depend on patch area and connectivity. This pattern also seems to hold for typical butterflies and grasshoppers [Maes & Bonte, unpub. data]. Because stenotopic spider species have narrow niche breadths and a reduced dispersal power, an increasing habitat fragmentation will even fasten their extinction rates, compared to more eurytopic species.

The geometry of habitat patches does not solely influence the distribution and population structure of spiders [and invertebrates]. Interpatch dispersal capacity will depend on dispersal mode and the related connectivity [permeability] of the matrix. More concrete, we can expect that a matrix consisting of rough vegetation will be experienced as a barrier for stenotopic species of grey dunes. For larger specialised species [having a restricted aerial dispersal capacity] as *Alopecosa fabrilis, A. barbipes, Pardosa monticola* and

Xysticus ninnii, cursorial dispersal is assumed to be the most important dispersal mode. Since the nature of the matrix will be a potential dispersal constraint, a restricted interpatch movement can be expected if grey dune habitats are located within a matrix of thick grassland, shrub or woodland vegetation. For smaller species with a relatively better developed aerial dispersal [species belonging to the *orbicularia* clades – see chapter III.2] and a limited cursorial dispersal [passive hunting techniques, smaller sizes], the nature of the matrix is probably of less importance as dispersal mainly occurs by ballooning. It is, however, not impossible that a tall matrix vegetation [woodland or high scrub vegetation] can restrain an effective aerial dispersal because ballooning individuals may be 'captured' in the matrix before they are able to reach suitable habitat.

Based on the results for our model species *Pardosa monticola*, dispersal is certainly influenced by the quality of the habitat and the landscape configuration. If intensive grazing results into a dramatic reduction of the grassland height, habitat quality will decrease for some species, and result in higher 'random' cursorial emigration patterns. In well-connected grasslands, this increased exchange of individuals [and genes] will stabilise population-genetic structure and metapopulation dynamics. If, however, intensive grazing occurs in strongly isolated patches, increased levels of emigration will speed up local extinction [Allee-effect]. For aerial dispersal, indications of local adaptation were found in this study. Both prenatal maternal and innate effects influence the performance of the pre-dispersal tiptoe behaviour and indicate that habitat fragmentation can lead to a decrease in dispersal rates, possibly because genes, associated with dispersal disappear in isolated populations [Dieckmann *et al*. 1999]. As a consequence, behavioural traits narrowly linked to dispersal may in addition to the morphological design of species [and populations], evolve towards less mobile phenotypes in fragmented terrestrial habitats [Van Dyck & Matthysen 1999]. At least one spider species is able to change its behavioural design in function of a changing landscape. The restriction of dispersal in isolated fragments will decrease direct mortality costs. If, however, genetic exchange completely disappears, an increased amount of inbreeding can act as a high cost, resulting in lower fitness within the population [David 1998], which again decreases the growth rate of the population, resulting in higher extinction chances. Therefore, it remains possible that, although local adaptation potentially counteracts direct mortality costs due to unsuccessful emigration, inbreeding will lead to an increased extinction rate in strongly isolated populations. Within one landscape type, variation in dispersal behaviour seems to be maternally determined. Connecting and enlarging grey dunes, will improve habitat quality and change the frequency of mothers with dispersing offspring. A fast change in the landscape is hence expected to induce optimal dispersal strategies within short time intervals. At a larger geographic scale, however, ballooning dispersal appears to be adaptive and determined by costs and benefits reflected within the landscape configuration. This adaptation towards the landscape also has consequences for species introduction, if characteristics of the source habitat and landscape are ignored. The introduction of spiders into vacant patches is, however, purely hypothetical and certainly not recommendable. Spiders, being generalist predators, are no keystone species [*sensu* Simberloff 1998] within terrestrial ecosystems and are easily replaced by species from the same guild.

These previously described patterns certainly hold for spiders from grey dunes along the Flemish coast. However, care has to be taken in extrapolating or generalising these findings to similar fragmented habitats in or beyond our region. In Europe, similar patterns of population dynamics are possible in spiders from fragmented heathland and chalk grassland, especially because many of the studied species also occur in these. Even if the geometry of suitable habitats appears to be similar, matrix vegetation will certainly be different. Therefore, if Euclidean interpatch distances are similar, patch connectivity will be different and responsible for different population-dynamical mechanisms. Although probably less relevant at regional scales, selection pressures related to the environment [differences in the dispersal window] may also differ and result in different dispersal [ballooning] strategies. This may certainly be real outside temperate Atlantic regions. The possible existence of different adaptive mechanisms in other environments makes extrapolation towards spiders from other fragmented habitats as fens, [salt]marshes and woodlands very dangerous. Illustrative are *e.g.* indications of a complete reduction of aerial dispersal capacity in stenotopic forest species, as found for *Oedothorax gibbosus* [Bonte & Vanacker, unpub. data] and *Pardosa saltans/lugubris* [Richter 1971]. Further research on the validation of our findings towards a larger spectrum of species and habitats is hence of primordial importance before general conclusions in function of nature conservation can be made.

An optimal conservation policy for the specific spider [and arthropod] fauna in coastal grey dunes of Flanders should hence aim for:
Restoration of grey dunes in an open landscape, where patch size and connectivity [which is of course species-dependant] are high.
Conserving sufficient internal structural variation by restoring aeolic dynamics and extensive grazing of larger herbivores.
Retaining sufficient 'rough vegetation', preferably as 'islands' into a grey dune landscape [an inversion of the current landscape] for conservation of endangered invertebrates restricted to these vegetation and for juvenile development of [some] species bound to grey dunes in the adult life-phase.

Perspectives for future research

Our results demonstrate that *dispersal* and *habitat quality* are key-aspects for organisms to settle and survive in fragmented habitats. In this thesis, however, only some aspects of spider dispersal were investigated and many questions remain to be answered. Especially ballooning dispersal needs further investigation because of its importance in shaping species distribution at local, regional and global scale. Within the evolutionary and ecological framework of dispersal behaviour, the following items need special attention:

- As both theoretical and empirical studies illustrate how different ***selective mechanisms*** may influence the evolution of dispersal, the ***validation*** and ***interaction*** between these different mechanisms in determining spider ballooning dispersal needs further investigation. More specifically, the validation of the selective mechanism generated by habitat fragmentation needs to be tested for species from other heavily fragmented habitats like saltmarshes, chalk grasslands and woodlands. More detailed empirical research on the interaction with other theoretical possible selection mechanisms like inbreeding avoidance and kin-competition is still a blank page in the literature on dispersal. The importance of these mechanisms for the evolution of intra- and interspecific variation in cursorial dispersal, inclusive the dropping behaviour of spiderlings from the maternal abdomen, resulting in ***other dispersal distances***, has neither been studied. ***Distinguishing*** between long-term and short-term selective forces is hence a major challenge, because it is questionable whether long-distance dispersal has actually evolved to colonise new sites, and is not a byproduct of selection for short-distance dispersal [Ronce *et al.* 2001].

- Dispersal propensity in spiders appears to be very ***plastic*** and to a large amount apparently randomly expressed within populations. Since prenatal, postnatal environmental conditions and proximate factors potentially influence the performance [distance, timing, latency] of dispersal, these need to be investigated in ***carefully designed laboratory experiments.*** Especially the study of ***reaction norms***[26] in function of varying pre- and postnatal environmental conditions seems promising. Also, the potential ***trade-off*** in spiders to chose between fast dispersal after birth with little experience of the environment and a delay of dispersal after an increased experience with the environment seems important in understanding dispersal motivation. Within this evolutionary framework, it seems important to estimate the ***magnitude*** of the additive-variation [***h?***] for ballooning dispersal and the importance and generality of maternal conditional effects. How does the '***window***' of dispersal [meteorological conditions for long or short flights, season, life stage] affect the ballooning behaviour of spiders [ballooning latency, duration of tiptoe-behaviour, possibly related to the length of the silk threads, number of repeated take-offs] towards environmental triggers and how does it change under different selective pressures within and between regions of different altitude and latitude is another important evolutionary-ecological topic and may be important for the understanding of invasive dispersal patterns in function of climate change.

[26] *The mapping of the genotype onto the phenotype as a function of the environment. It is usually expressed as a plot of phenotypic values against environmental values. The reaction norm of a genotype is the full set of phenotypes that that genotype will express in interaction with the full set of environments in which it can survive. If reaction norms are non-parallel, a Genotype x Environment interaction is present [Stearns 1992].*

- ***Interactions*** of spider [ballooning] dispersal with ***life history***-traits and ***morphological*** traits have not yet been detected. Relevant for ballooning dispersal is the potential relation between dispersal propensity and reproductive output, growth speed and the size of the silk glands. Within the framework of the latter, the relevance of energetic costs due to the production of [multiple] silk threads, in interaction with variable environmental conditions, may be important in constraining or restraining ballooning dispersal.

- Most studies focus on the propensity of spiders to disperse by ballooning. However, the adjustment of body morphology and thread-length can potentially ***control*** their ***flight*** and hence ***landing***. Since the chance of reaching suitable habitat appears to be a strong selective force, inter- and interspecific variation of flight control possibly counteracts the assumed random dispersal and landing. Carefully conducted field experiments should enable us to answer this question.

- According to Weyman *et al.* [2002], future research within the framework of pest control should additionally focus on ***external moderators*** of ballooning dispersal like semiochemicals associated with the prey and with plants damaged by herbivorous prey and on ***resource exploitation benefits*** [exploitation of ephemeral habitats where competition with other predators is minimal]. Especially the development of reliable spatial dynamical models of spider dispersal on arable farmland is to be achieved, because the knowledge of these pest predator dynamics is necessary for sustainable agricultural practices.

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SAMENVATTING

Dit proefschrift beschrijft het voorkomen van spinnen in grijze kustduinen in de Vlaamse en omliggende kustduinen langs de Noordzee en de evolutionaire-ecologische gevolgen van inter- en intraspecifieke variatie in het dispersiegedrag ervan.

Grijze duinen, dit zijn gefixeerde kustduinen met een kruidachtige vegetatie, bestaan uit vegetaties die gedomineerd worden door mossen en lage kruiden en grassen. Ecologisch gezien vormen ze de droge component van het gestresseerde duinlandschap. Tijdens de laatste decennia raakte dit habitattype sterk gefragmenteerd door verruiging en vervilting. En het is binnen de context van dit veranderende duinlandschap dat we [i] de variatie in de spinnengemeenschappen en [ii] het dispersiegedrag van spinnen hebben gedocumenteerd. In het eerste deel [hoofdstukken II.1-II.4] behandelen we de ruimtelijke variatie van spinnengemeenschappen in het gehele duinecosysteem van de Vlaamse kust en de regionale en lokale variatie binnen grijze duinen langs de Noordzee. In het tweede deel [hoofdstukken III.1-III.8] gaan we dieper in op enkele ecologische-evolutionaire facetten van inter- en intraspecieke variatie in dispersiegedrag van spinnen.

In ***hoofdstuk II.2*** wordt de samenstelling van de spinnengemeenschappen in de Vlaamse kustduinen onder de loep genomen. Die blijkt bepaald te zijn door variatie in vegetatiestructuur [successie], atmosferische en bodemvochtigheid en de aanwezigheid van zowel anthropogene als natuurlijke verstoring. Voor alle onderscheiden vegetatietypes kunnen indicatorsoorten geïdentificeerd worden. Variatie binnen de gemeenschappen is afhankelijk van de respectievelijke gemiddelde oppervlaktes van de habitatvlekken waarover ze beschikken. Vooral spinnengemeenschappen van sterk gefragmenteerde habitats met kleine oppervlaktes, b.v. grijze duinen, worden gekenmerkt door een grote verscheidenheid in soortensamenstelling en kunnen bijgevolg als onstabiel bestempeld worden. Uit grondiger onderzoek naar het voorkomen van soorten in deze grijze duinen blijkt dat niet de totale soortenrijkdom, maar het aantal specifieke [stenotope] soorten afneemt naarmate de oppervlakte kleiner wordt. Dit patroon is waarschijnlijk het gevolg van toenemende randeffecten, van een kleiner aanbod aan microhabitats of van hogere uitstervingskansen van lokale populaties in kleine fragmenten.

De samenstelling van spinnengemeenschappen van grijze duinen is eveneens afhankelijk van locale en geografische variatie in vier regio's met een verschillende geologische geschiedenis en landschapsstructuur langsheen de Noordzee [***hoofdstuk II.3***]. Deze variatie kan vooral toegeschreven worden aan verschillen in zanddynamiek en connectiviteit met andere xerotherme habitats zoals heiden en kalkgraslanden. Stenotope soorten van dynamische duinen vinden we vooral terug in de duingebieden langs de Vlaamse en Noord-Franse kust [= de Boulonnais], terwijl typische soorten van heiden en kalkgraslanden respectievelijk de duingebieden van Noord-Holland en de Boulonnais koloniseerden. Deze soorten zijn afwezig in het jonge en geïsoleerde duinlandschap van de Vlaamse kust. We besluiten dat regionale variatie in de spinnengemeenschappen van grijze duinen, het gevolg is van lokale landschapskarakteristieken [zanddynamiek], de breedtegraad en de connectiviteit met andere xerotherme habitattypes. Zowel landsschapsgeschiedenis als [beperkingen in] dispersie bepalen naar alle waarschijnlijk het voorkomen van spinnen in grijze duinen.

Kortom, de spinnengemeenschappen van zowel het gehele Vlaamse duinecosysteem als van de grijze duinen langs de Noordzee in het bijzonder worden gestructureerd door ecologische tijd, verstoring en mechanismen die gerelateerd zijn aan de productiviteit van het habitat [vegetatiesuccessie, vochtigheid en habitatheterogeniteit] [***hoofdstuk II.4***]. Aangezien bovengronds levende spinnen mobiel zijn, bepalen randeffecten zowel variatie binnen als tussen de verschillende habitattypes.

Een en ander doet vermoeden dat dispersie cruciaal is voor de bepaling van distributiepatronen van spinnensoorten op kleine en grote schaal. Daarom onderzoeken we in het tweede deel van het proefschrift de populatiedynamiek en een aantal evolutionaire-ecologische aspecten van dispersie bij spinnen.

Onder gestandaardiseerde laboratoriumomstandigheden hebben we inter- en intraspecifieke variatie in luchtdispersie bestudeerd, meer bepaald het tiptoe-gedrag, dat vooraf gaat aan de eigenlijke dispersie door middel van *ballooning*. Ballooning [vrij vertaald “ballonvaren”] is een passieve dispersiemethode waarbij spinnen, vastgehecht aan een spindraad, meegevoerd worden in luchtstromingen. Deze vorm van dispersie is als het ware een loterij in de lucht; de afwezigheid van controle over de vluchtroute is immers een belangrijke kost voor lange-afstandsverplaatsingen in een gefragmenteerd landschap. Ballooninggedrag wordt dus verondersteld op een andere manier te zijn geëvolueerd dan actievere dispersiewijzen, waarbij organismen wel controle kunnen uitoefenen op hun verplaatsing. In ***hoofdstuk III.2*** tonen we voor 29 spinnensoorten met een verschillende mate van gebondenheid aan het grijze-duinhabitat aan dat natuurlijke selectie een goed ontwikkeld ballooningvermogen bevoordeligt, als het risico om te belanden in een gunstig habitat groter is dan de kans om een ongeschikt habitat te bereiken. We kunnen dat afleiden uit de negatieve relatie tussen de neiging om te disperseren via ballooning en de mate van habitatspecialisatie. Onze bevindingen zijn in overeenstemming met recente theorieën dat dispersie geselecteerd kan worden door generalisten als risicospreiding, terwijl het tegengeselecteerd kan worden bij habitatspecialisten.

Om het voorkomen van soorten in gefragmenteerde grijze duinen te verklaren hebben we vervolgens die soortspecifieke data betreffende de neiging tot ballooning afgewogen tegenover nichebreedte [habitatspecialisatie] en vlekconfiguratie [***hoofdstuk III.3***]. De aanwezigheid van soorten in deze fragmenten blijkt enkel bepaald te worden door het dispersiepotentieel ervan en de interactie tussen vlekconnectiviteit en –oppervlakte. Nichebreedte daarentegen blijkt geen verklarende factor te zijn voor extra variatie in distributiepatronen. Bovendien tonen onze bevindingen aan dat dispersie onze perceptie van de fundamentele niche van soorten beïnvloedt, en dat source-sink en metapopulatiedynamiek een grote impact hebben op het voorkomen van soorten in een gefragmenteerd landschap.

In een volgende hoofdstuk hebben we de intraspecifieke variatie in tiptoegedrag onderzocht bij *Erigone atra* [***hoofdstuk III.4***]. Concreet hebben we nagegaan wat de invloed is van genetische verwantschap [familie-effecten] en postnatale omgevingsomstandigheden op de latentietijd tot het vertonen van tiptoegedrag van deze soort. Allereerst bleek uit een drie-weken durend experiment, waarbij de spinnen enkel gevoed werden tijdens de eerste dag van de week, de latentie tot ballooning een lage herhaalbaarheid vertoonde na periodes van één week. Gedurende de eerste week van het experiment daalde de latentietijd significant naarmate de uithongering toenam. Dit patroon werd echter niet meer waargenomen tijdens de twee laatste weken van het experiment. Na kortere tijdsintervallen van 1 uur vertoonde de ballooninglatentie echter wel een hoge herhaalbaarheid.

Door nakomelingen van verschillende families onder twee voedings- en temperatuurs-omstandigheden op te kweken hebben we daarnaast onderzocht of maternale en postnatale omgevingsvariatie tijdens de juveniele ontwikkeling een invloed heeft op de expressie van het tiptoegedrag. Uit dit experiment blijkt dat omgevingseffecten in veel hogere mate de variatie verklaren dan het familie-effect. De latentietijd ligt lager bij spinnen die opgekweekt worden bij een temperatuur van 20°C dan bij die opgekweekt bij 15°C. Daarenboven wordt de latentie eveneens significant beïnvloed door het voedingsregime: goed gevoede individuen vertonen namelijk een sneller tiptoegedrag dan hun slecht gevoede soortgenoten. Temperatuur en voedingsregime interageren daarenboven significant met elkaar, wat de aanwezigheid van verschillende reactienormen aantoont. De expressie van ballooninglatentie hangt dus in sterke mate af van het actuele voedingsniveau, de voedingsgeschiedenis en de voedsel- en temperatuursomstandigheden tijdens de juveniele ontwikkeling. Variatie die toegeschreven kan worden aan genetische verwantschappen [additieve en/of maternale effecten] is laag, maar biologisch relevant.

In de hoofdstukken III.5-III.7 spitsen we ons toe op de populatiedynamiek, de cursorische en ballooningdispersie bij de duinwolfspin *Pardosa monticola*. De ruimtelijke populatiedynamiek bij deze soort, die voorkomt in gefragmenteerde graslanden van de Vlaamse kustduinen [duingebied tussen Duinkerke en Nieuwpoort], wordt behandeld in ***hoofdstuk III.5***. Op basis van gegevens over de al dan niet aanwezigheid ervan in habitatvlekken in 1998 en in 2000 hebben we met behulp van incidentiefunctiemodellen, patronen in het voorkomen, de kolonisatie en de uitsterving ervan onderzocht. Merk-hervangstexperimenten tonen aan dat maximale cursorische dispersie-afstanden 280 meter zijn in mosduinen en 185 meter in duingrasland en dat de connectiviteit in de matrix afhankelijk is van de vegetatiestructuur. Deze habitatafhankelijke potentiële cursorische dispersie-afstanden en de theoretisch bepaalde potentiële ballooningafstand werden samen met geografische afstanden tussen de verschillende vlekken in een connectiviteitsmaat geïntegreerd. Met behulp van een meervoudige regressie-analyse hebben we uiteindelijk aangetoond dat het voorkomen van *P. monticola* bepaald wordt door habitatkwaliteit en de connectiviteit, zoals bepaald voor ballooningdispersie. Habitatkwaliteit en cursorische connectiviteit verklaren variatie in korte-termijn kolonisatieprocessen terwijl het uitsterven van populaties vooral stochastisch gebeurt.

Allozymelektroforese heeft daarnaast ook aangetoond dat genetische variatie en variabiliteit tussen populaties laag is. Deze discrepantie tussen de geschatte lage dispersiemogelijkheden en de indirecte schatting van genuitwisseling F_{ST} bewijst dat de populatiegenetische structuur van deze soort bepaald wordt door historische populatiedynamiek en/of historische gen-uitwisseling via ballooning.

In het incidentiefunctiemodel wordt uitgegaan van vlekonafhankelijke willekeurige dispersiepatronen. Mogelijke gedragsmechanismen die aan de basis liggen van een wijziging van dergelijke dispersie, zijn echter slecht gedocumenteerd, vooral voor arthropoden. We vermoeden echter dat de veronderstelde willekeurige dispersierichting niet opgaat voor heel wat diersoorten waarbij dispersie en beweging gebaseerd zijn op het maken van directe gedragskeuzes. Om dat na te gaan hebben we interdemische variatie in zowel cursorische als ballooningdispersie bij *P. monticola* meer in detail onderzocht.

In ***hoofdstuk III.6*** gaan we dan ook dieper in op de relatie tussen habitatkwaliteit en ballooning bij juveniele *P. monticola* die afkomstig zijn van moederdieren uit duingraslanden met een verschillende connectiviteit en prooivoorspelbaarheid. Uit de studie van het al of niet voorkomen van tiptoegedrag kunnen we afleiden dat postnatale omgevingsfactoren [uithongering], prenatale, maternale effecten en evolutionaire factoren de expressie van dit gedrag beïnvloeden en dat habitatfragmentatie tot een gereduceerd dispersievermogen kan leiden. Een mogelijke verklaring hiervoor is dat de genen die verantwoordelijk zijn voor een dergelijk gedrag, verdwenen zijn uit geïsoleerde populaties. Doordat zowel de maternale conditie als fitness daalden met een toenemende isolatiegraad, kunnen we op basis van datzelfde experiment besluiten dat selectie tegen dispersie een zekere risicospreiding inhoudt. Binnen populaties hebben we echter tegengestelde patronen waargenomen, aangezien een vermindering van lokale habitatkwaliteit, zoals gereflecteerd in de maternale conditie, de neiging tot dispersie bevordert. Gedragskenmerken gerelateerd aan dispersie kunnen dus net zoals morfologische kenmerken in een gefragmenteerd landschap evolueren tot minder mobiele fenotypes.

Aan de hand van veldexperimenten hebben we vervolgens bij *P. monticola* de veranderingen in de cursorische emigratie onderzocht in functie van de habitatkwaliteit [***hoofdstuk III.7***]. Tegelijkertijd hebben we het oriëntatiegedrag op verschillende afstanden van de rand van het grasland in de mosduinmatrix geobserveerd tijdens twee relevante perioden in de adulte levensfase, namelijk de periode van copulatie en reproductie. Hieruit blijkt dat de cursorische activiteit stijgt in de habitat van lage kwaliteit, waar de populatiedensiteit ook laag is, en dat dit resulteert in een verhoogde emigratie. In dit habitat was de vrouwelijke cursorische activiteit zelfs hoger dan die van de mannetjes, waardoor vrouwelijke *P. monticola* in dezelfde mate emigreerden als mannetjes. In de populaties van hoge kwaliteit, en met een hogere populatiedichtheid, wordt de emigratie daarentegen duidelijk door het mannetje gedomineerd. Noch de mannetjes noch de vrouwtjes kunnen zich in mei, d.i. de periode tijdens welke het grasland even hoog staat als het mosduin, oriënteren ten opzichte van de rand van het grasland. In juni, daarentegen, hebben we geen oriëntatie t.o.v. het graslandhabitat opgemerkt in de lage-densiteitspopulatie [lage differentiële vegetatiehoogte ten opzichte van de mosduinmatrix], maar wel bij vrouwtjes tegenover het hogekwaliteitsgrasland, waar de vegetatie duidelijk hoger is dan die van het mosduin. Aangezien deze oriëntatie enkel gebeurde op korte afstand van het grasland, wijzen de gevonden oriëntatiepatronen op de aanwezigheid van een geslachtsafhankelijke visuele perceptie of op een geslachtsafhankelijke motivatie om terug te keren naar het gunstige graslandhabitat. Verhoogde emigratie als gevolg van een verhoogde mobiliteit en het ontbreken van oriëntatie ten opzichte van het graslandhabitat duiden dan weer op het voorkomen van een Allee-effect in graslanden van lage kwaliteit met lage populatiedichtheid.

We komen op basis van de verschillende deelonderzoeken uit het tweede deel tot de conclusie dat dispersie door ballooning bij spinnen van de gefragmenteerde grijze kustduinen tegen geselecteerd wordt indien hun kansen om een geschikt habitat te bereiken, dalen [***hoofdstuk III.8***]. De neiging tot ballooning is bijgevolg heel laag in sterk geïsoleerde populaties of bij sterk gespecialiseerde soorten van het grijze duin. Daarenboven wordt dispersie bij spinnen in hoge mate beïnvloed door omgevingsspecifieke factoren, zowel voor ballooning [nl. acuut voedseltekort, voedselstress en temperatuur tijdens de juveniele ontwikkeling, maternale habitatkwaliteit en landschapsconfiguratie] als voor cursorische dispersie [nl. habitatkwaliteit en aard van vegetatieovergang tussen habitat en matrix]. Nogal wat variatie blijkt niet te verklaren te zijn, zoals aangetoond voor ballooning bij *Erigone atra* en cursorische dispersie bij *Pardosa monticola*. Die sterk veranderlijke dispersietendensen zijn in overeenstemming met de gemengde evolutionaire stabiele strategie, waarbij ieder individu van een genetisch monomorfe populatie een willekeurige dispersiestrategie kiest uit een gemeenschappelijke probabileitsverdeling, die aanpasbaar is aan de lokale omgevingsomstandigheden, inclusief maternale effecten. Deze ogenschijnlijke willekeurige strategie kan uiteraard wel het resultaat zijn van door ons moeilijk te bepalen omgevingseffecten. In tegenstelling tot de hoge onverklaarbare en vlekspecifieke variatie, tonen algemene modellen, gestoeld op een uniforme willekeurige dispersie, aan dat dispersie het voorkomen van soorten en populatiedynamiek beïnvloedt. Interdemische variatie in dispersie is dus belangrijk vanuit een ecologisch-evolutionair perspectief, maar van minder belang voor synecologische patronen. Uiteraard zijn interacties tussen individuele variatie in dispersie en populatiedynamiek, zoals bediscussieerd in dit proefschrift, veel complexer dan die opgenomen in de gebruikte modellen. Het integreren van gedragsmechanismen zou, op zijn minst voor enkele soorten, de biologische relevantie van populatiedynamische modellen verhogen. Vooral voor sterk bedreigde soorten kunnen betere inzichten in populatiedynamische processen leiden tot betere beschermingsmaatregelen ervoor.

De implementatie van onze onderzoeksresultaten in maatregelen ten behoeve van natuurbeheer in de Vlaamse en omliggende kustduinen langs de Noordzee houdt voornamelijk het behoud in van habitats gebonden aan het gestresseerde en dynamische duinlandschap [***hoofdstuk IV.1***]. Zo zouden een extensief begrazingsbeheer en het herstel van eolische dynamiek de connectiviteit en het oppervlak van de grijze duinen aanzienlijk doen toenemen. En die verandering in de landschapsconfiguratie verzekert vooral het voortbestaan van typische stenotope soorten die over een slecht ontwikkeld dispersievermogen beschikken.

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Dispersal is crucial in structuring species distribution, population structure and species ranges at large geographical scales or within local patchily distributed populations. The knowledge of dispersal evolution, motivation, its effect on metapopulation dynamics and species distribution at multiple scales is poorly understood and many questions remain unsolved or require empirical verification. In this thesis we contribute to the knowledge of dispersal, by studying both ecological and evolutionary aspects of spider dispersal in fragmented grey dunes. Studies were performed at the individual, population and assemblage level and indicate that behavioural traits narrowly linked to dispersal, considerably show [adaptive] variation in function of habitat quality and geometry. Dispersal also determines spider distribution patterns and metapopulation dynamics. Consequently, our results stress the need to integrate knowledge on behavioural ecology within the study of ecological landscapes.

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