DISTRIBUTION OF SPIDERS IN COASTAL GREY DUNES - SPATIAL PATTERNS AND EVOLUTIONARY-ECOLOGICAL IMPORTANCE OF DISPERSAL

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Grey dune, known as "Fixed coastal dunes with herbaceous vegetation" include Atlantic moss dominated dunes as well as dune grassland and is ecologically the dry component of the "stressed dune landscape". At present, rough grass- and scrub encroachment result in a strong fragmentation and patchily distributed habitat configuration. By using spider as bio-indicators, I aimed to document changes in species distribution and dispersal behaviour within the context of this changing landscape.

These topics are discussed into two major parts. In the first part (chapters II.1-II.4) we report on variation in spider assemblages within the entire coastal dune system of the Flemish coast and on regional and local variation within grey dune assemblages along the North Sea. In the second part (chapters III.1-III.8) some ecological and evolutionary consequences of inter- and intraspecific variation in dispersal are addressed.

In *chapter II.2* we investigated spider assemblages in the ecosystem of the Flemish coastal dunes. These appear to be 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 habitats 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 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. Assemblages from grey dunes also show considerable local and regional variation within four distinct dune regions along the North Sea, with a different geological history and landscape structure (*chapter II.3*). 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.

In conclusion (*chapter II.4*), we demonstrated that spider assemblages within the entire ecosystem of the Flemish coastal dunes and from grey dunes in four different regions are generally influenced by ecological time, disturbance and mechanisms related to the productivity of the habitat (vegetation succession, humidity, habitat heterogeneity). Because epigeic spiders are mobile, edge effects additionally determine variation within and between assemblages. 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, some aspects of its evolutionary and ecological importance are addressed in part III.

Inter- and intraspecific variation in aerial dispersal was studied under standardised laboratory conditions by observing the pre-ballooning tiptoe-behaviour. This 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 is expected to evolve in a different way than morphological traits, directly linked to active dispersal. In *chapter III.2*, we demonstrated for 29 species from grey dunes, having different levels of habitat specialisation, that selection benefits a well-developed ballooning behaviour if the risk of landing in an unsuitable habitat is lower than the probability of reaching suitable habitat. This can be concluded from the negatively relationship between ballooning performance and habitat specialisation. These findings are concordant with recent insights that dispersal is selected as risk spreading in generalists, while it is selected against in specialist species.

These data on ballooning propensity are used to investigate the relative contribution of dispersal, habitat specialisation and patch configuration in shaping species distribution patterns (*chapter III.3*). Since species distribution patterns may been explained by Hutchinson's niche theory, metapopulation theory and source-sink theory, we linked data on the occurrence of species in 19 grey dune patches with data on patch isolation, patch area and the specific level of habitat specialisation. In coastal grey dunes from Flanders, spider 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. 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.

Intraspecific variation in tiptoe-behaviour was investigated in *Erigone atra*, our first model species *(chapter III.4)*. We investigated the influence of common lineage (family effect) and postnatal environmental conditions on latency to initiate preballooning tiptoe behaviour (ballooning latency). 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, by rearing 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. Variation due to the family (additive variation and/or maternal effects) was low but biologically significant.

In the chapters III.5-III.7, we focussed on population dynamics, cursorial and aerial dispersal in the dune wolf spider *Pardosa monticola*.
The spatial population dynamics of this species, inhabiting patchily distributed grasslands in the Flemish coastal dunes from Belgium and Northern France are documented in *chapter II.5*. Patterns in patch occupancy, colonisation and extinction were investigated with incidence function models using field survey data from 1998 and 2000. Mark-recapture experiments revealed maximum cursorial dispersal distances of 280 m for moss dunes and 185 m for higher dune grassland and different connectivity levels of the matrix vegetation. 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.
In the previously discussed incidence model, patch-independent estimates of random dispersal were used to define patch connectivity. Behavioural mechanisms underlying alterations of such movements are however poorly understood, especially for arthropods. The assumed uniform random dispersal directions, might however, not be applicable to a large set of species for which dispersal and movement involve at least some element of decision-making. Therefore, variation of behavioural responses in function of the habitat was investigated for both cursorial and aerial dispersal.

In *chapter III.6*, 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. 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 as revealed from maternal condition, 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.

In *chapter III.7*, we investigated *Pardosa monticola*'s mobility and emigration pattern in the 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 quadrate 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). Our field experiments confirmed the hypothesis that increased activities of this dune wolf spider in a low-density habitat result in higher emigration rates. 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 orientation towards the patch border suggest the presence of an Allee effect in low-density patches.

In conclusion (*chapter III.8*), 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 reduced in strongly isolated populations or in species with a high degree of specialisation to the grey dune habitat and selected against, if the landscape becomes more heterogeneous and fragmented. In addition, 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 variations 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 a mixed Evolutionary Stable Strategy, 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.

The 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. In contrast to the 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. 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 and 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.

Implementation of our results into a proper strategy for nature management (*chapter IV.1*), highlights the conservation of habitats related to the stressed and dynamic dune landscape. Not only habitats of endangered species are in this way conserved, but it additionally implicates that mechanisms related to sand dynamics and herbivory are retained. Under these conditions, the configuration of grey dune patches will evolve towards higher connectivity and patch areas and will ensure the occupancy of stenotopic spider species, which are characterised by a low dispersal.