THE TEMPORAL AND SPATIAL RELATIONSHIP BETWEEN STENOTOPIC DWARF SPIDERS (ERIGONINAE: ARANEAE) AND THEIR PREY (ISOTOMIDAE: COLLEMBOLA) IN COASTAL GREY DUNES: A NUMERICAL AGGREGATIVE RESPONSE OR COMMON MICROHABITAT PREFERENCE?

by

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ABSTRACT

During 1999-2001, we investigated the spatial and temporal relationship between stenotopic dwarf spiders and their springtail prey in coastal grey dunes. This habitat is characterised by severe microclimatological fluctuations that influence the spatial and temporal distribution of epigeic invertebrates. In three types of grey dune vegetation, where springtails showed different temporal abundance patterns, a positive relationship was observed between the phenology of the palatable springtails and stenotopic dwarf spiders. In particular, the relationship with female spiders, which depend highly on prey for reproduction, was very significant.

A similar spatial aggregation exists for both prey and predator. Their presence was influenced by the same soil and vegetation characteristics. Two mechanisms are assumed to be responsible for this similar distribution; a common, independently developed habitat preference or a numerical response from the spiders in the presence of prey. After correction for intra-correlations, the relationship between prey and predator was non-significant and hence more likely to be the result of common microhabitat preferences.

KEY WORDS: Araneae, Collembola, time series analysis, coastal grey dune, prey-predator relation, Belgium.

1. INTRODUCTION

The microclimate on grey dunes along the Flemish coast is very extreme, and summer drought and extremely high temperatures can be limiting factors for the survival of plants and animals. As a result of these harsh circumstances, inhabiting plant species flower in early spring (winter annuals) or go into a non-active drought stage during the summer. Many invertebrates show analogue adaptations and are only active during the winter.

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period; they occupy more buffered habitats during the summer (BONTE et al., 2000) and show high thermal and drought resistance (ALMQQUIST, 1970, 1971). For springtails, only Cryptopygus thermophilus can be found in xerothermic dune habitats during the summer and is assumed to be highly resistant to summer drought and high temperatures (BONTE et al., 2002). In grey dunes, Collembola are the main prey for dwarf spiders because of their small size and high abundance. However, not all springtail species are suitable as prey for spiders (and other carnivorous invertebrates). MESSER et al. (2000) gave an overview of toxic and unpalatable Collembola species: in particular, species of the family Poduridae are never eaten because of bad tasting substances in the cuticle. The observed dominant species, Isotoma viridis, is one of the most preferred prey items for dwarf spiders since it has an optimal size and leads to high spider fitness (MARCUSSEN et al., 1999; TOFT, 1999). Isotoma viridis has two generations per year in mesotrophic dune grasslands with a well developed grass-layer, but is represented only in one generation in oligotrophic grey dunes, dominated by mosses (BONTE et al., 2002). Besides the unpalatable or toxic springtails, relatively small sized prey is ignored (NENTWIG & WISSEL, 1989).

Prey-predator relationships are mainly investigated in agricultural systems, within the framework of pest-control. In these systems, springtails are the most important prey for web-building Linyphiinae and sit-and-wait predators of the Erigoninae (overview, NYFFELER, 1999). Erigoninae of arable fields especially prefer isotomids (with a tendency for larger individuals), as demonstrated in field and laboratory experiments by ALDERWEIRELDT (1994).

In coastal grey dunes, dwarf spiders can occur during the entire season. Stenotopic species are considered to be true inhabitants that are adapted to these low productive and extreme habitats, while eurytopic species are good aeronauts blown into these habitats by coincidence, and will not survive or stay because of food limitation and desiccation.

Besides temporal occurrence patterns, springtails occur in large aggregations in grey dunes (BONTE et al., 2002). Efficient foraging by their predators must therefore imply a mechanism in which these predators (in this case, stenotopic dwarf spiders) should find these aggregates either by direct attraction to their prey or by the shared preference for common microhabitats. Females, in particular, should benefit from an optimal prey location since food limitation affects fitness (BRADLEY, 1993; TOFT, 1999; KREITER & WISE, 2001).

In this paper we investigate whether the temporal distribution of palatable springtails is related to that of stenotopic spiders and to what extent these predators show an aggregative numerical response on a small spatial scale.
MATERIAL AND METHODS

Palatable springtails and their dwarf spider predators


Temporal covariation between the phenology of stenotopic Erigoninae and palatable springtails

The temporal relationship between palatable springtails (Collembola) and their predators (stenotopic spiders) were investigated in the dune area ‘The Westhoek’ in De Panne (West-Flanders, Belgium). Temporal patterns were investigated by a year-round sampling campaign with small pitfall traps (testing tubes with a diameter of 12 mm) for Collembola and with larger pitfall traps (110 mm diam.) for spiders from April 1999 to April 2000 in three grey dune habitats (table 1). In each station, ten small and five large pitfall traps were linearly placed and emptied approximately monthly (15 times during the entire sampling period). A 6% formaldehyde-soap solution was used for the conservation of the

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Distance to the sea</th>
<th>Soil formation</th>
<th>Coverage bare sand</th>
<th>Height vegetation</th>
<th>Main plant species</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phleo-Tortuletum typicum</em></td>
<td>30 m</td>
<td>0-1 cm</td>
<td>30-50%</td>
<td>0-2 cm</td>
<td><em>Tortula ruralis ruraliformis</em> <em>Phleum arenarium</em> <em>Ononis repens</em> <em>Rosa pinninellifolia</em> <em>Avenula pubescens</em> <em>Festuca rubra</em> <em>Tortula ruralis ruraliformis</em> <em>Phleum arenarium</em> <em>Cladonia spec.</em></td>
</tr>
<tr>
<td><em>Taraxaco-Galietum veri</em></td>
<td>30 m</td>
<td>8-12 cm</td>
<td>0-5%</td>
<td>3-12 cm</td>
<td><em>Tortula ruralis ruraliformis</em> <em>Phleum arenarium</em> <em>Ononis repens</em> <em>Rosa pinninellifolia</em> <em>Avenula pubescens</em> <em>Festuca rubra</em> <em>Tortula ruralis ruraliformis</em> <em>Phleum arenarium</em> <em>Cladonia spec.</em></td>
</tr>
<tr>
<td><em>Phleo-Tortuletum cladonietosum</em></td>
<td>1100 m</td>
<td>0-1 cm</td>
<td>30-50%</td>
<td>0-2 cm</td>
<td><em>Tortula ruralis ruraliformis</em> <em>Phleum arenarium</em> <em>Ononis repens</em> <em>Rosa pinninellifolia</em> <em>Avenula pubescens</em> <em>Festuca rubra</em> <em>Tortula ruralis ruraliformis</em> <em>Phleum arenarium</em> <em>Cladonia spec.</em></td>
</tr>
</tbody>
</table>
sampled animals. All epigeic springtails were identified to the species or genus level (Bonte et al., 2002).

Since both the trapping period and the number of effective pitfalls (sand accumulation resulted in 29 non-useful traps during the entire sampling period) differed during the total sampling period, we standardised the total numbers per period to the numbers caught per trap per day (numbers/trap/day) in order not to have biased analyses.

Spatial relation between the numbers of stenotopic dwarf spiders and palatable springtails

The spatial relationship was investigated with pitfall-traps with a diameter of 39 mm. One hundred traps were placed in a grid, with an inter-trap distance of 1 metre, in a structurally homogeneous grey dune which was differentiated in soil depth (organic A-layer, from here on referred to as soil formation), vegetation height and vegetation coverage. Due to the structural homogeneity, microclimatological circumstances are assumed to be similar, so aggregative patterns should result from a numerical response or from common microhabitat preferences (soil depth, small differences in vegetation height). Soil formation was measured because it influences the water catchment capability strongly (Krabbenborg et al., 1983). Trampling of the grazing cattle/horses destroyed four traps; hence only 96 traps were active from 15 March – 15 April 2001. The microhabitat-associated parameters were measured in a radius of 15 cm around each trap. The depth of the organic soil-A-layer was measured to the nearest cm. All springtails and stenotopic dwarf spiders were counted and identified. All palatable prey and stenotopic dwarf spiders were considered as two functional groups for analysis.

Data analysis

In the analysis of both the temporal and spatial relationships, the numbers of springtails and spiders are Poisson-distributed. Since time series are highly influenced by temporal autocorrelation with different time lags, time series analysis (Box-Ljung statistics) was applied for the detection of autocorrelation for catches at time \( t \) with catches of time \( t \pm 1 \) for all phenology data and for the comparison by cross-correlation of the different phenology patterns between the number of palatable springtails and the stenotopic dwarf spiders (all sexes, males and females separately). The data were transformed to ranks for the study of the spatial relationship (Spearman partial correlation) in which a master factor, which showed high correlations with the two investigated parameters, was
kept constant. When multiple comparisons were conducted, Bonferroni-corrections were applied.

All analyses were performed with the statistical package STATISTICA 5.1.

RESULTS

Temporal covariation between the phenology of stenotopic Erigoninae and palatable springtails

A low and, after Bonferroni-correction, insignificant temporal autocorrelation was only found for the total number of palatable springtails in the *Phleo-Tortulae cladonietosum* grey dune (table 2), so we can consider catches at time $t$ independent from those at time $t - 1$. Cross-correlation with spider presence at the same period $t$ revealed, with the exception of the male spiders-relation in the *Taraxaco-Galietum* and *Tortula classicum* vegetation, significant correlation (table 3). In the three habitat types, the correlation was always higher for females than for males. Figs 1-3 represent the temporal distribution of these female dwarf spiders with the palatable springtails in the three investigated grey dunes.

Spatial relation between the numbers of stenotopic dwarf spiders and palatable springtails

The number of stenotopic dwarf spiders and the number of palatable springtails are at first sight positively significantly correlated ($R = 0.339$; $p < 0.01$), although not after Bonferroni-correction. Both variables are also related to different soil and vegetation variables (table 4), which are,

<table>
<thead>
<tr>
<th>Grey dune type</th>
<th>Palatable springtails</th>
<th>Stenotopic dwarfspiders males</th>
<th>Stenotopic dwarfspiders females</th>
<th>Stenotopic dwarfspiders total</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Phleo-Tortula classicum</em></td>
<td>+0.176</td>
<td>+0.185</td>
<td>+0.271</td>
<td>-0.311</td>
</tr>
<tr>
<td><em>Phleo-Tortula cladonietosum</em></td>
<td>+0.462</td>
<td>-0.246</td>
<td>+0.359</td>
<td>+0.257</td>
</tr>
<tr>
<td><em>Taraxaco-Galietum</em></td>
<td>+0.415</td>
<td>+0.373</td>
<td>+0.411</td>
<td>+0.366</td>
</tr>
</tbody>
</table>
TABLE 3
Cross correlations between phenology patterns of the palatable springtails and the stenotopic dwarfspiders. Significant relations after Bonferroni-correction are indicated with *.

<table>
<thead>
<tr>
<th>Grey dune type</th>
<th>Gender</th>
<th>r</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taraxaco-Galietum</td>
<td>males</td>
<td>0.513</td>
<td>0.050</td>
</tr>
<tr>
<td>Taraxaco-Galietum</td>
<td>females</td>
<td>0.622</td>
<td>&lt;0.010*</td>
</tr>
<tr>
<td>Taraxaco-Galietum</td>
<td>total</td>
<td>0.561</td>
<td>&lt;0.010</td>
</tr>
<tr>
<td>Phleo-Tortula cladonietosum</td>
<td>males</td>
<td>0.894</td>
<td>&lt;0.010*</td>
</tr>
<tr>
<td>Phleo-Tortula cladonietosum</td>
<td>females</td>
<td>0.916</td>
<td>&lt;0.010*</td>
</tr>
<tr>
<td>Phleo-Tortula cladonietosum</td>
<td>total</td>
<td>0.891</td>
<td>&lt;0.010*</td>
</tr>
<tr>
<td>Phleo-Tortula classicum</td>
<td>males</td>
<td>0.545</td>
<td>&lt;0.010</td>
</tr>
<tr>
<td>Phleo-Tortula classicum</td>
<td>females</td>
<td>0.828</td>
<td>&lt;0.010*</td>
</tr>
<tr>
<td>Phleo-Tortula classicum</td>
<td>total</td>
<td>0.706</td>
<td>&lt;0.010*</td>
</tr>
</tbody>
</table>

Fig. 1. Phenology of palatable springtails (bars) and female stenotopic dwarfspiders (line) in the *Phleo-Tortuletum typicum* grey dune.

in turn, strongly intercorrelated. After controlling for the soil-formation (which is the most strongly related environmental factor) or for grass coverage (which is more likely to be a common correlated factor), the
Fig. 2. Phenology of palatable springtails (bars) and female stenotopic dwarfspiders (line) in the Taraxaco-Galietum veri grey dune.

Fig. 3. Phenology of palatable springtails (bars) and female stenotopic dwarfspiders (line) in the Phleo-Tortuletum cladonietosum grey dune.
Spearman correlation coefficients between the number of stenotopic dwarfspiders and palatable springtails per pitfall and the measured soil- and vegetation characteristics. Significant relations after Bonferroni-correction are indicated with *.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Stenotopic dwarfspiders</th>
<th>Isotomid springtails</th>
</tr>
</thead>
<tbody>
<tr>
<td>B-layer depth (cm)</td>
<td>-0.385</td>
<td>-0.623</td>
</tr>
<tr>
<td>Bare sand coverage (%)</td>
<td>-0.073</td>
<td>0.038</td>
</tr>
<tr>
<td>Grass coverage (%)</td>
<td>-0.327</td>
<td>-0.560</td>
</tr>
<tr>
<td>Moss coverage (%)</td>
<td>0.295</td>
<td>0.530</td>
</tr>
<tr>
<td>Vegetation height (cm)</td>
<td>-0.208</td>
<td>-0.378</td>
</tr>
</tbody>
</table>

relationship between the number of springtails and spiders deteriorates (part. $R_{\text{soil}} = 0.134$; part. $R_{\text{grass}} = 0.186$; $p > 0.05$). A schematic overview of the different relations between soil formation, vegetation structure and the number of spiders and springtails is presented in fig. 4.

DISCUSSION

Although our results are based on pitfall captures and not on absolute sampling techniques, the time series analyses indicate that the temporal activity of palatable springtails significantly corresponds with those of their predators. Both palatable Collembola species and stenotopic dwarf spiders are absent from the Phleo-Tortula vegetation in the summer period, but are present during that season in comparable, though not analogue Taraxacum-Galietum vegetation. Spider and springtail phenologies covary significantly positively in the three separately investigated grey dune types; the relation with female dwarf spiders in particular was remarkable. In the adult stage, female spiders, especially, need beneficial feeding conditions to reproduce (Bradley, 1993; Toft, 1999; Kreiter & Wise, 2001). This covariation led us to suspect a numerical response of particularly females to high prey abundances. We should, however, interpret this relationship carefully since pitfall catches depend on both species density and activities and do not indicate a straight relationship between prey and predator abundances. The absence of stenotopic dwarf spiders in the summer on the Phleo-Tortula vegetation is mainly responsible for the identified relations. Factors other than covariation with prey abundance, such as microclimate, soil moisture or vegetation composition, can affect prey and predator densities in the same way. The Taraxoco-Galietum is characterised by higher vegetation height and coverage and a better-developed
Fig. 4. Spatial Spearman correlation coefficients between the presence of palatable springtails, stenotopic dwarfspiders and the measured vegetation- and soil characteristics. $R_{abc}$ indicates partial correlation coefficient controlled for abc; significance levels: *: $p < 0.01$; **: $p < 0.001$. 
soil formation, which can influence alone, or in combination with prey abundance, the presence of stenotopic dwarf spiders. Phenology patterns of prey and predator thus covary, mainly as the result of absence of both prey and predator during the dry summer period. This should not indicate strictly a numerical response, but can also be an effect of unsuitable dry and hot meteorological conditions, which affect the presence of all small, sedentary invertebrates (large surface/mass ratio).

The fact that both predator and prey densities are affected by common environmental factors becomes clearer from the spatial relation analysis. Grass coverage and soil formation, in particular, affect the aggregation of both isotomid springtails and dwarf spiders negatively. Controlling for soil formation and grass coverage makes the direct positive correlation between the number of springtails and spiders non-significant. The aggregative response in grey dunes is more likely the result of common habitat preference instead of a strict prey-predator relationship. On the contrary, as expected by Bonte et al. (2002), both spiders and springtails react negatively during this season to soil formation and grass coverage. These species thus aggregate strongly in function of the moss coverage (at least during this season) and associated microhabitat characteristics, and not of the soil moisture content which is related to soil formation (Krabbenborg et al., 1983).

Aggregation of spiders and their prey is also related to common vegetation structure in the webspider *Argiope keyserlingi* (Bradley, 1993), in which both seasonal and spatial distribution patterns correlate highly significantly, as in our study. Harwood et al. (2001) also found that web locations of linyphiid spiders were positively associated with available food resources, but they were not able to understand the underlying mechanism of common microhabitat preferences of prey and predator aggregates. In other invertebrates (Coleoptera), the numerical response to prey abundances is also a result of interactions between time, prey quantity and prey quality (Carabidae & Staphylinidae: Monsrud & Toft, 1999; Coccinellidae: Osawa, 2000). In agricultural situations, Monsrud & Toft (1999) found a significant direct numerical response between aphids and active aphid feeders (Staphylinid and Carabid larvae).

Our field study thus indicates that the numerical response between springtail-feeding spiders and their prey cannot be attributed for certain to direct predator attraction. Small differences in habitat structure affect the distribution of both prey and predator in the same way. Laboratory experiments confirmed the fact that dwarf spiders do not react to chemical stimuli of prey (pheromones) or to direct visual contact (Bonte & Mertens, unpublished results). Apparently, the preference for the same microhabitat resulted in an optimal foraging strategy for collembolan-feeding dwarf spiders in habitats where prey occur at low densities
and in dense aggregates. Whether this analogue microhabitat preference resulted from evolutionary optimal foraging benefits is, however, still questionable.

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REFERENCES


