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SEASONAL AND DIURNAL MIGRATION PATTERNS OF THE SPIDER (ARANEAE) FAUNA OF COASTAL GREY DUNES

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Abstract

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The study of the grey dune species' phenology patterns revealed interesting data on the occupation of this xerotherm habitat by several spider species groups. Apparently stenotopic erigonid species are totally absent during the summer months. A possible explanation for this phenomenon is the lack of suitable prey (Collembola). Larger species of the Gnaphosidae, Thomisidae, Salticidae, Lycosidae and Araneidae are present during the summer. Of these *Haplodrassus dalmatensis* is characterised by clear seasonal migration from the litter border zone, where the juvenile development takes place, to the open grey dune as reproduction habitat. The smaller stenotopic erigonid species (*Typhochrestus digitatus*, *Pelecopsis nemoralis*) do not show a clear seasonal but instead a diurnal migration between these two habitats in their adult phase.

Introduction

An analysis via classification and ordination techniques of the spider fauna of the Flemish coastal dunes revealed several communities with a specific one for grey dunes (BONTE et al., in prep.). Of all investigated coastal dune habitats, grey dunes are characterised by the largest proportion of dune-specific spider species, which are all listed on the Flemish Red List of spiders (MAELFAIT et al., 1998). Examples of these are *Haplodrassus dalmatensis* (L. KOCH), *Zelotes longipes* (L. KOCH), *Micaria dives* (LUCAS), *Phlegra fasciata* (HAHN), *Alopecosa fabrilis* (CLERCK), *Arctosa perita* (LATREILLE), *Trichopterna cito* (O.P.-CAMBRIDGE) and *Walckenaeria stylifrons* (O. P.-CAMBRIDGE).

The microclimate on these grey dunes is very extreme. Especially summer drought and extremely high temperatures may be limiting factors for spider presence. ALMQUIST (1970, 1971) states that some typical dune-living spiders are characterised by high thermal tolerances and high resistance to desiccation, but he did not relate this to their microhabitat preferences in the Swedish coastal dunes.

Because of the extreme microclimatological conditions in the grey dune habitat, we expect there to be seasonal migration of the species from suitable microhabitats for juvenile development to the habitat that is suitable for reproduction. The latter is the place where adults are captured with pitfall traps. Since DE KEER et al. (1989) stipulated the importance of grass tussocks in intensively grazed pastures as hibernation sites and resting places for species of open habitats in relation to diurnal activity, similar migration patterns are expected to avoid unfavourable meteorological or biological conditions.

This paper presents data on the importance of the habitat interaction between the Creeping Willow (*Salix repens*) dwarf scrubs and the grey dunes in relation to juvenile development and both seasonal and diurnal migration activities of the stenotopic grey dune spider species.

Material and methods

These investigations were performed in the Flemish nature reserve “De Westhoek” in De Panne (West Flanders, Belgium). The grey dune vegetation belongs to the Tortulo-Koelerietalia (SCHAMINÉE et al., 1996), with typical higher plants such as *Phleum arenarium*, *Myosotis ramosissima*, *Erodium cicutarium ssp. dunense* and *Viola curtisii*. The vegetation is especially rich in mosses such as *Tortula ruralis ssp. ruraliformis* and *Ditrichum flexicaule* and the lichens *Cladonia furcata*, *Leptogium gelatinosum* and *L. lichenoides*. The border vegetation is dominated by *Salix repens* scrub with accompanying species such as *Monotropa hypopitys*, *Pyrola rotundifolia*, *Veronica officinalis* and *Viola hirta*. The inner shrub vegetation is dominated by *S. repens* and *Hippophae rhamnoides* with mainly *Calamagrostis epigejos* and *C. canescans* in the undergrowth. The total surface of the grey dune exceeds 1000 m². The *S. repens* scrubs surround the grey dune patches with a surface area varying between 30-150 m² and are characterised by a litter layer (maximum 3.5 cm deep) which is influenced by displacement by the wind.

From April 1997 till March 1998, the ground-active spider fauna was sampled by three pitfalls in the grey dune, three in the *S. repens* border zone and three in the inner shrubs. They had a diameter of 9.5 cm and were emptied fortnightly and refilled with a formaldehyde-water-soap solution. Additionally, 30 quadrat samples (20x20 cm²) per habitat type were taken in the first week of each month during the day. This sampling took place from November 1997 till October 1998. They were manually sorted and additionally extracted for ten days in Tullgren funnels. The litter dry weight of the border quadrat samples was determined for the months January till March 1998 (90 in total) by putting the extracted litter samples additionally 24 hours in an oven with a constant temperature of 80°C.

From 12-17 January 1998, 30 additional pitfalls with a diameter of 6 cm were operative: ten in the border zone, 10 at 30 centimeter and another 10 at three meter from the scrub zone in the grey dune. During this five day period, the pitfalls were emptied twice a day in order to study day and night activity of the winter-active species. The pitfalls were removed and emptied between one half hour before and one half hour after, respectively, sunrise (9.00 AM) and sunset (17.00 PM). On the 17 January 1998, 30 analogue quadrat samples were taken in the grey dune and in the border zone, both at midnight and noon. These 120 samples were again manually sorted and extracted in Tullgren funnels.

Results

Spider densities on the grey dune and in the Salix repens border zone: indication for seasonal migration?

The monthly spider density in the litter layer of the Creeping Willow border reached its maximum at the beginning of the winter and its minimum in the spring (Fig. 1), while spider densities on the grey dune were largest in October and lowest during June-July. In the litter zone, juveniles dominated the arachnofauna, while the grey dune was (at least during the day) exclusively inhabited by adult spiders at very low densities (1-10% of the total densities in the border zone). The significant density decline in the litter between December 1997 and January 1998, was remarkable, and was probably caused by a significant mortality due to frost.

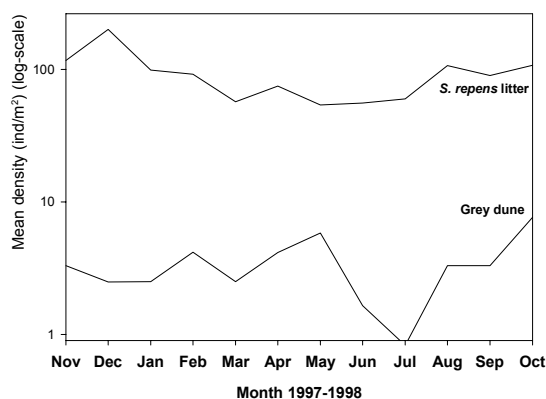


Fig. 1. Monthly densities (ind./m²) of spiders on the Grey dune and in the *Salix repens* border zone (litter) during the period November 1997-October 1998.

All monthly densities were characterised by a much larger standard deviation (not listed), suggesting an aggregated distribution of the spiders in the litter (and on the grey dune, although at very low mean densities). The aggregated character of the winter-active erigonid species *Typhochrestus digitatus* (O.P.-CAMBRIDGE) and *Pelecopsis nemoralis* (BLACKWALL) and the total number of spiders can be explained as a response to litter depth (Fig. 6). Both species, as well as the total number, were significantly correlated with litter dry weight (*T. digitatus*: $R=0.637$, $P<0.01$; *P. nemoralis*: $R=0.263$, $P<0.05$; total spiders: $R=0.565$, $P<0.01$, Pearson correlation). The aggregation of the other common winter species could not be explained as a function of litter depth (*Haplodrassus dalmatensis*: $R=0.032$; *Ceratinopsis romana* (O.P.-CAMBRIDGE): $R=0.175$, for both $P>0.05$, Pearson correlation). For these species other biotic or abiotic parameters must be responsible for the aggregated distribution pattern in the border zone.

Of these abundant species, *C. romana*, *P. nemoralis* and *T. digitatus* stayed in the litter during their juvenile and adult phases (see Figs 2-4). Only a small number of adult individuals

were captured on the grey dune by means of quadrats. *Haplodrassus dalmatensis*, on the contrary, was characterised by juvenile development in the litter, while adults were almost exclusively found on the grey dune surface (Fig. 5). This suggests a clear seasonal migration

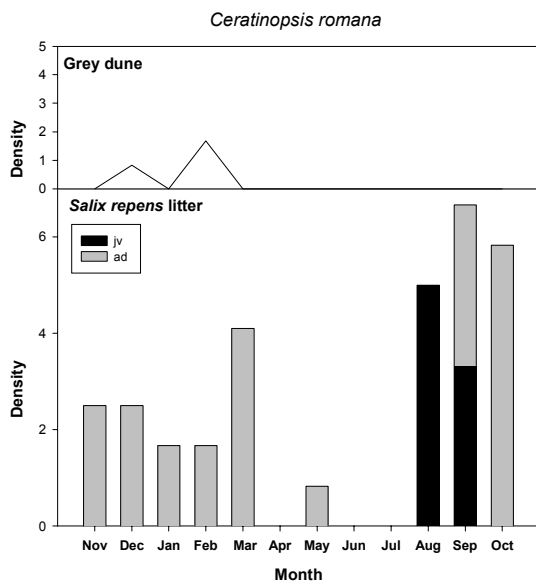


Fig. 2. Monthly densities (ind./m²) of juveniles (jv) and adults (ad) of *Ceratinopsis romana* in the *Salix repens* litter (bars) and on the grey dune (only adults: line) during the period November 1997-October 1998.

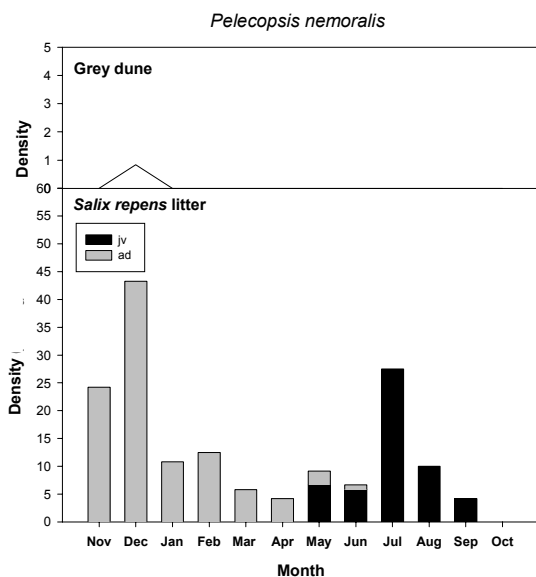


Fig. 3. Monthly densities (ind./m²) of juveniles (jv) and adults (ad) of *Pelecopsis nemoralis* in the *Salix repens* litter (bars) and on the grey dune (only adults: line) during the period November 1997-October 1998.

from the litter to the grey dune for mating and reproduction. Because of the larger surface of the grey dune, the density increase did not fully compensate for the density decrease in the litter in which the juvenile instars were concentrated during their development.

Other species that reached monthly densities higher than one per m² on the grey dune, on at least one occasion, were *Arctosa perita* and *Xysticus sabulosus* (HAHN). The latter were almost completely absent from the border zone in the adult stage, while their juvenile development was clearly situated in this habitat. Although the numbers were too small for certainty, there appeared to be also a seasonal horizontal migration from the litter to the open grey dune for reproduction. The high juvenile densities of *Dictyna arundinacea* (LINNAEUS), *Philodromus cespitum* (WALCKENAER) and *Theridion bimaculatum* L. in the litter, with a maximum during the winter period (resp. 4.17 ind./m², 5.83 ind./m² and 4.17 ind./m²), are also interesting. These species are known to inhabit the shrub layer during the season of leaf growth and then they apparently undergo a vertical seasonal migration from the shrub to the litter layer for hibernation.

Mobility patterns as deduced from pitfalls and quadrats

Since we collected data about spider distribution by using both pitfalls and quadrat samples, we were able to determine the absolute species mobility by dividing the numbers in pitfalls (for months in which the species reached their highest abundance in pitfalls) by the mean species densities based on quadrats.

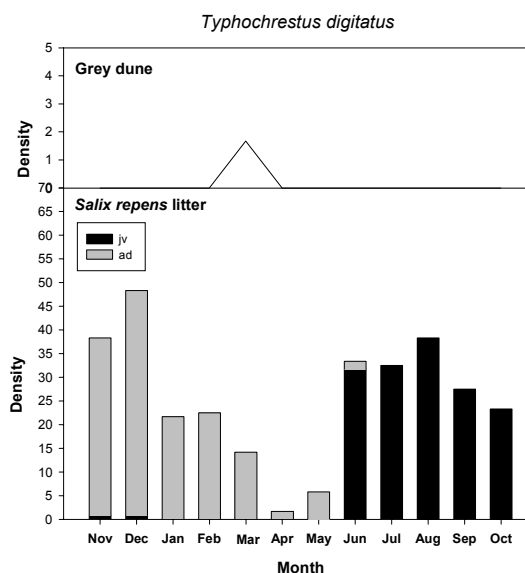


Fig. 4. Monthly densities (ind./m²) of juveniles (jv) and adults (ad) of *Typhochrestus digitatus* in the *Salix repens* litter (bars) and on the grey dune (only adults: line) during the period November 1997-October 1998.

This was calculated for the most abundant species and is visualised in Fig. 7. Species which were caught in high numbers in pitfalls but which were not observed in quadrats reached the highest specific mobility value: *Arctosa perita*, *Erigone atra* BLACKWALL, *Erigone dentipalpis* (WIDER), *Lepthyphantes tenuis* (BLACKWALL), *Meioneta rurestris* (C. L. KOCH), *Sitticus saltator* (O. P.-CAMBRIDGE.), *Trochosa terricola* (THORELL) and *Xerolycosa miniata* (C. L. KOCH). Species with a moderate activity were *Haplodrassus dalmatensis* and *Xysticus sabulosus*. The other mentioned species were less mobile judging by these calculations. We should, however, take into account that the numbers taken from the quadrats and the pitfalls

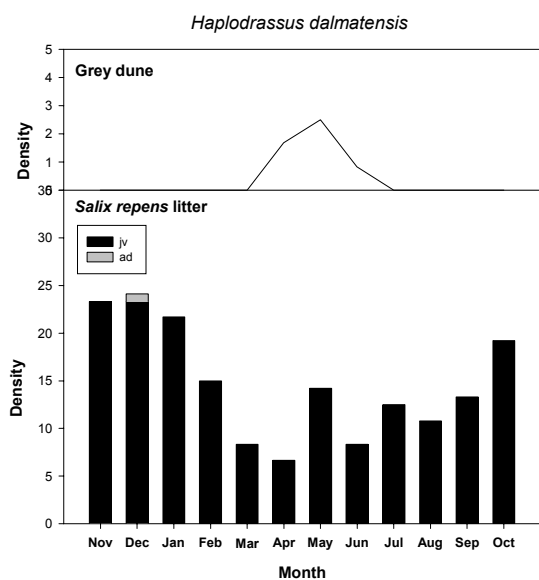


Fig. 5. Monthly densities (ind./m²) of juveniles (jv) and adults (ad) of *Haplodrassus dalmatensis* in the *Salix repens* litter (bars) and on the grey dune (only adults: line) during the period November 1997-October 1998.

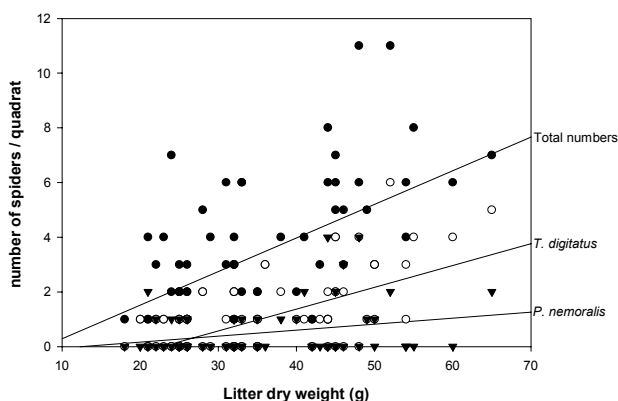


Fig. 6. Relation between spider densities and *Salix repens* litter dry weight, as derived from 30 400 cm²-quadrat samples /month during the period January-March 1998.

Fig. 7. Mobility values of the most abundant spider species in the *Salix repens*-Grey dune mosaic. Ceraroma: *Ceratinopsis romana*, Clubtriv: *Clubiona trivialis*, Erigatra: *Erigone atra*, Erigdent: *Erigone dentipalpis*, Hapl dalm: *Haplodrassus dalmatensis*, Lepttenu: *Lepthyphantes tenuis*, Meioure: *Meioneta rures-tris*, Pelenemo: *Pelecopsis nemoralis*, Stemline: *Stemonyphantes lineatus*, Tapiprae: *Tapinocyba praecox*, Typhdigi: *Typhochrestus digitatus*, Xystsabu: *Xysticus sabulosus*, Sittsalt: *Sitticus saltator*, Trocterr: *Trochosa terricola*, Arctperi: *Arctosa perita*, Xeromini: *Xerolycosa miniata*.

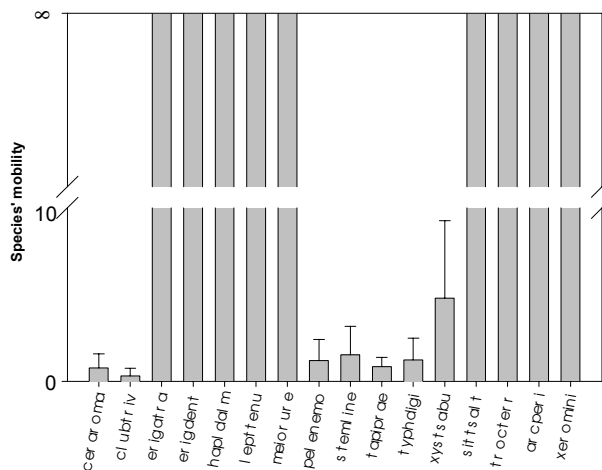
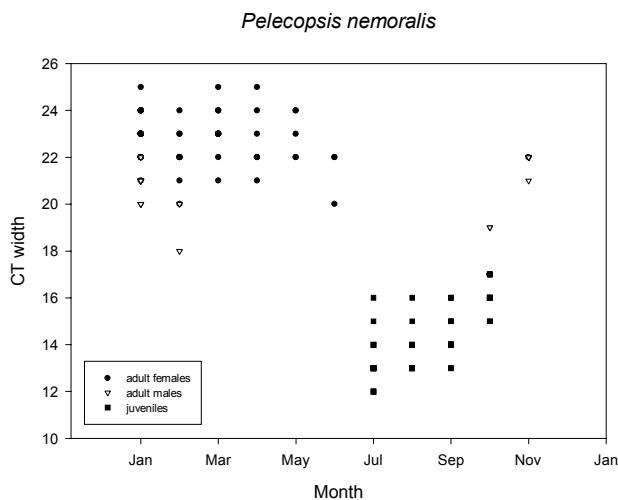


Fig. 8. Seasonal growth of *Pelecopsis nemoralis* as derived from monthly CT-width measurements (units).



were not completely comparable since the pitfalls registered activity during the night and the day, while the quadrats were only taken by day.

Life history of Pelecopsis nemoralis, Typhochrestus digitatus and Haplodrassus dalmatensis

As we measured the cephalothorax (CT) width of all the captured adult and juvenile spiders, we were able to reconstruct the life cycle of the dominant species, by plotting the width against the capture period (cf. TOFT, 1976, 1978, 1979).

Pelecopsis nemoralis and *Typhochrestus digitatus* are typical examples of species with an annual life cycle with reproduction in the winter period and juvenile development from May-June onwards (Figs 8, 9). Although total number of juvenile *C. romana* were too small for the reconstruction of its seasonal growth, an analogue life cycle can be expected based on the seasonal presence of both juveniles and adults in the grey dune-*S. repens* mosaic (Fig. 2).

The life cycle of *Haplodrassus dalmatensis* can be determined as mixed annual-bien-nial. Apparently, there is a period of juvenile appearance from August till May. Juveniles of

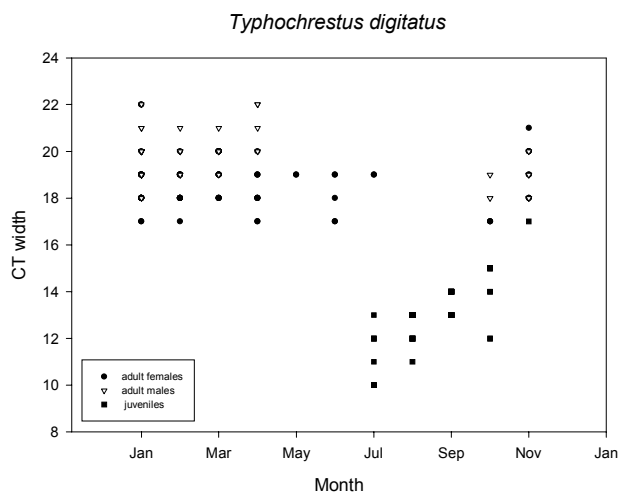


Fig. 9. Seasonal growth of *Typhochrestus digitatus* as derived from monthly CT-width measurements (units).

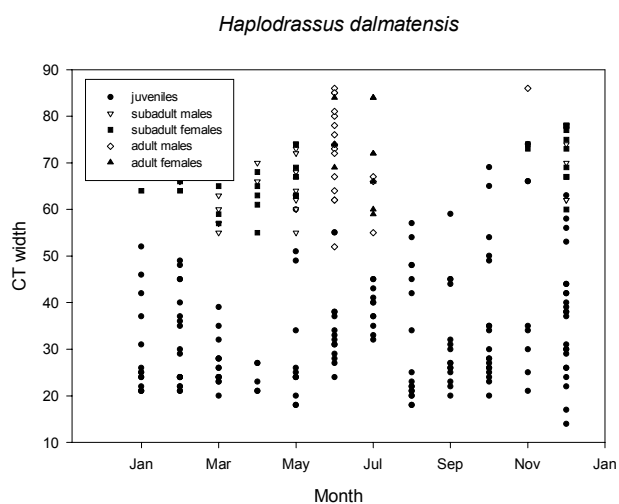


Fig. 10. Seasonal growth of *Haplodrassus dalmatensis* as derived from monthly CT-width measurements (units).

Fig. 11. Horizontal migration and day-night activity of *Typhochrestus digitatus* as derived from intensive pitfall trapping during 5 days and nights in the *S. repens* litter and resp. 30 cm and 300 cm from the *S. repens* border.

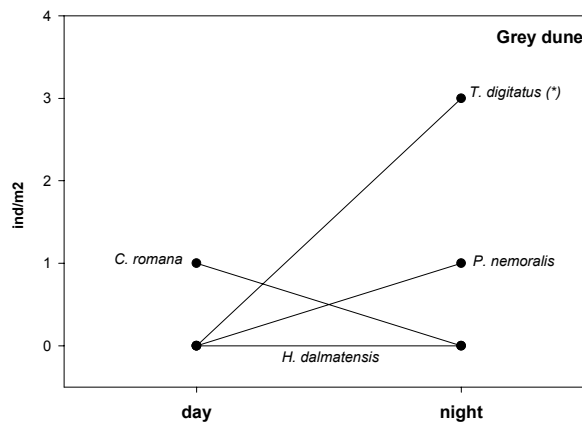
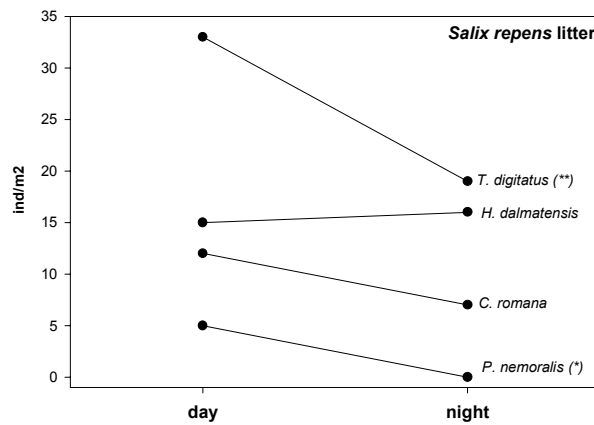
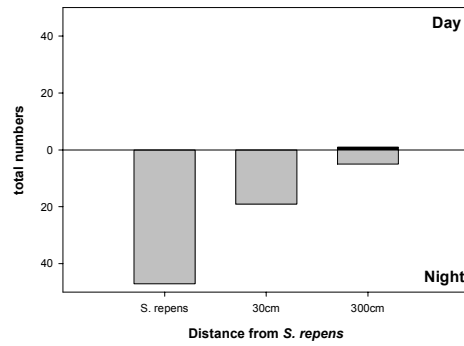


Fig. 12. Changes in spider densities (*Ceratinopsis romana*, *Pelecopsis nemoralis*, *Typhochrestus digitatus* and *Haplodrassus dalmatensis*) in the *Salix repens* litter (A) and the grey dune (B) during the night and the day. Significance levels (**): $P < 0.05$; (*): $P < 0.1$.

the summer and early autumn generation will hibernate in a third or fourth instar (Fig. 10) and become adult in the following spring. Juveniles of the winter and spring will grow to a subadult stage by the next winter, and become adult in the following spring. This spread of juvenile appearance results in there being several developmental periods and consequently a great variance of adult size.

Diurnal migration in a dwarf scrub-grey dune mosaic during the winter period

In order to study possible diurnal migration of the winter-active erigonid spiders *Ceratinopsis romana*, *Pelecopsis nemoralis* and *Typhochrestus digitatus*, a short intensive day-night sampling campaign was organised with pitfalls and quadrat samples in both the grey dune and the *Salix repens* border zone. Since the day and night periods were not equal, the number of individuals of the species caught with the pitfalls were transformed into 12 hours night and day by multiplying the numbers caught during the day with 12/7 and those of the night with 12/15.

The three target species were mainly caught during the night, but the night activity was only significant for *T. digitatus* ($P < 0.01$, Welche's t-test). For the latter, a clear declining activity pattern is visible in relation to increasing distance from the border zone (litter, 30 cm and 300 cm from *S. repens*: Fig. 11), suggesting a preference for the grey dune border zone during the night.

Comparison of the mean densities of *T. digitatus* between day and night in both the grey dune and the border zone revealed a clear and significant ($P < 0.05$, Welche's t-test) density decline in the border zone during the day in comparison with the night densities. Conversely, a density increase was observed in the grey dune area during the night ($P < 0.1$, Welche's t-test), suggesting, for this species, a diurnal migration from the border zone to the grey dune at night. The same migration pattern was observed for *P. nemoralis*, although this was not significant at the 0.05-level ($P < 0.1$, Welche's t-test). The other species did not show any migration trend between the border zone and the grey dune.

Discussion

Analysis of the composition of the arachnofauna of the Flemish grey dunes showed that only 23.5% of species belonged to the dune-specific fauna. Other captured species were migrants with high a migration rate achieved by ballooning (BONTE et al., 1999) or typical species of the surrounding dense grass and shrub vegetation (BONTE et al., in prep.). For the latter, grey dunes are apparently no great barriers for migration between shrub or grass patches in the dune landscape.

The major function of the scrub-border zone is as a juvenile-development habitat. All juveniles of the observed typical species stayed in *S. repens* litter until they became adult. Even juveniles of species with a biennial life cycle stayed in the litter during the period of

adult activity. Once the mature life stage was reached, adults of the larger typical species migrated permanently to the grey dune. In our studied site however, adults of the small erigonid species (*Typhochrestus digitatus* and probably *Pelecopsis nemoralis*) stayed in the litter zone during the day but moved to the open grey dune during the night.

A similar behaviour was noted by DE KEER et al. (1989) in an intensively grazed pasture. They found a clear diurnal migration in diurnal species, which preferred the short grazed sites. The nocturnal species were consequently immobile and confined to the denser grass tussocks. Since, in this study, the quadrat samples were always taken during the day, a permanent presence of the nocturnal adults *Haplodrassus dalmatensis* should be accepted. The clear habitat separation of this biennial species between the juvenile and the adult instars is different from the normal habitat use recorded for species with an annual life cycle. Cannibalism of the juvenile instars by the adults is possibly a driving force behind this different pattern of habitat use.

The complete absence of stenotopic summer-active erigonid species in the grey dune arachnofauna is remarkable. This may possibly be related to food availability in the grey dunes. Since springtails (Collembola) are the main prey items for the smaller species, their dynamics on the soil surface may determine the presence and survival of the potential predators. KOEHLER et al. (1995) found six dominant springtail species on the Schiermonnikoog grey dunes (The Netherlands). Unfortunately, they give no data on the seasonal fluctuations of the species in this habitat. The lack of active Collembola on the grey dune surface during the summer months is however quite likely: BAUER (1979) found, under laboratory circumstances, a clear vertical springtail migration in the soil in response to a moisture gradient. The lack of springtails at the desert surface in New Mexico (USA) was studied by MACKAY et al. (1987). They proved that this was the result of two processes; vertical migration and cryptobiosis during the unfavourable conditions (i.e. high temperatures, low soil and air humidity).

The larger spider species can survive the summer months, since larger prey items are still available: POLLET, GROOTAERT (1996) found three ground-active *Medetera*-species (Dolichopodidae) in relatively large densities on the grey dune surface. *Medetera*-species were observed as prey for *Xerolycosa miniata* and *Xysticus kochi* THORELL (BONTE, unpubl.). The immobility of winter-active erigonids contrasts with the high mobility rate of summer-active representatives. Since web-building was never observed by any of the mentioned species, this may be a confirmation for the high availability of prey during the winter (less mobility is necessary for prey-capture), while the high mobility of the summer-active species may be a result of the activity needed for active hunting for the very scarce preys.

Possibly, the small size of species in the Erigonidae may be a potential limiting factor for erigonid presence during the summer on the grey dunes (large surface/volume ratio and higher vulnerability to desiccation). This should, however, be of minor influence because of the presence of even smaller juveniles in the border litter and the possible diurnal horizontal migration and night-activity of adults (as observed during the winter).

Finally, we can conclude that the maintenance of these border zones is of primordial importance for the typical grey dune species. Care should be taken with rigorous shrub removal and especially the *S. repens* border zones should be conserved.

Acknowledgements

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