

Lack of homeward orientation and increased mobility result in high emigration rates from low-quality fragments in a dune wolf spider

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Summary

1. 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 was applied in combination with absolute density estimates by means of quadrat sampling. 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.
2. Our field experiments confirm the hypothesis that increased activities of a dune wolf spider in a low-density habitat result in higher emigration rates.
3. The diffusive emigration rates, which are higher close to the patch border, and 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.
4. 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 3 m, females also orientated randomly.
5. The pattern of differentiated homeward orientation behaviour indicates that it results from visual perception of high contrast borders by the females but not by the males or by sex-differentiated motivation to return to the core habitat.
6. Increased emigration rates as a result of higher spider mobility together with the absence of visual orientation towards the patch border suggest the presence of an Allee effect in low-density patches.

Key-words: Allee effect, dispersal, field experiment, *Pardosa monticola*, sexual variation.

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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 mechanisms may not be applicable to a large suite 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

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mechanisms that increase an organisms' ability to recognize suitable habitat patches and minimize unplanned or unexpected emigration in certain stages of its life cycle (Freaque 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.* 2003a), mainly related to mate-searching behaviour in males and foraging behaviour in gravid females (Maelfait & Baert 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 the 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, low humidity and very low or absent prey availability during summer (Provoost *et al.* 2002; Bonte unpublished data). Previous studies (e.g. Morse 2002) showed that orientation in species of this genus is mainly visually based, although the 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.* 2003a). We hypothesize that cursorial activity is lower in high-density habitats and that this results in lower diffusion rates throughout the season.

Materials and methods

STUDY SPECIES

The wolf spider, *P. monticola*, a widespread species in Europe and Asia, occurs typically 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.* 1998; 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). The species is the only occurring *Pardosa* within the habitat and, as other species from this genus, is cursorial, nomadic and non-territorial (Morse 1997; Bonte & Maelfait personal observation). Because of the non-territorial behaviour, movements of individuals (e.g. males) depend only on decision-making, based on criteria as vegetation features, microclimate and mate availability and not on inter- and intraspecific antagonistic reactions. Ballooning dispersal occurs rarely (Bonte *et al.* 2003b) 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.* 2003a), the selected grassland patches could be considered as sufficiently separated, with negligible movement interference between the patches.

We conducted standardized, biweekly counts between May 1 and June 14 2000 in 30 1-m² quadrats placed randomly 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./m² (further referred to as low density population, L), 1.23 ind./m² and 1.66 ind./m² (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 differed significantly 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 (Maelfait & Baert 1975), unbiased period specific mobility estimates (within and between grassland patches) were obtained by dividing the number of trapped males and females after each biweekly sampling period by their mean density in the core habitat (estimated independently, see above) at the start of the same biweekly 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 and 16 May 2000 and 18–20 June 2000, a total of 72 pitfall traps (4 cm diameter) 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.* 2003a), 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 one to five individuals at the centre of each circular plot and pitfalls

were checked every 30 min. Trapped individuals were removed from the experiment, whereas non-trapped individuals were released in the same or another experimental plot until 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 1996). 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 vs. 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 1996).

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 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 was female mobility 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

Table 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 d.f.	Den d.f.	<i>F</i>	<i>P</i>
Patch	2	262	64.64	< 0.0001
Distance	2	262	64.50	< 0.0001
Sex	1	262	4.21	0.042
Patch × distance	4	258	1.09	0.364
Patch × sex	2	262	3.07	0.049
Distance × sex	2	256	0.17	0.845
Patch × distance × sex	4	252	0.51	0.729

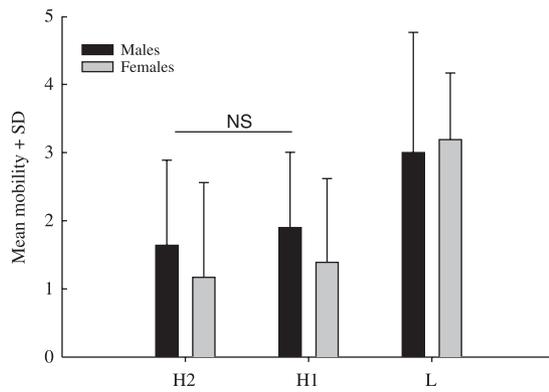


Fig. 1. Levels of cursorial mobility by male and female *P. monticola* in three grassland patches differing in population density; L = low density, H1 and H2 = high density (see text for details).

significantly higher in population L compared to the high-density patches H1 and H2, with the latter two being not significantly different (Fig. 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. 2).

VARIATION IN HOMEWARD ORIENTATION

Results of the orientation experiments are summarized in Table 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 vs. distant) (Fig. 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 $P > 0.05$). Similarly, no differences occurred between local and non-local individuals (edge: $F_{1,76} = 0.66$; 1 m: $F_{1,81} = 0.002$; NS).

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, characterized by low vegetation height and hence poor quality (Bonte *et al.* 2003a), results in increased

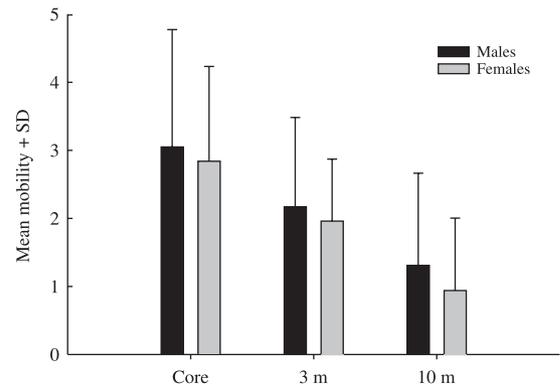


Fig. 2. Levels of cursorial mobility by male and female *P. monticola* in the core habitat and at 3 and 10 m from the grassland edge into the moss matrix outside the core habitat.

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 3 m 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 demonstrated previously 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 unsuitable 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 microclimatic conditions in this matrix (Bonte, Van Heuverswyn & Mertens 2002).

Table 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 egg sacs; Fem + eggs = females with egg sacs; native = individuals from local population; foreign = individuals from distant population

Period	Sex–reproductive status (population)	Circle	n	μ (95% CI)	r	
May	Males (native)	Patch	43	348.63°	0.14	
		Border	50	137.81°	0.17	
		1 m	74	323.83°	0.10	
		3 m	47	351.06°	0.16	
	Fem – eggs (native)	Patch	49	277.12°	0.13	
		Border	57	356.40°	0.19	
		1 m	57	346.31°	0.20	
		3 m	33	305.38°	0.04	
	June	Males (native)	Patch	38	89.81°	0.13
			Border	19	46.70°	0.24
			1 m	16	16.39°	0.37
			3 m	20	294.82°	0.18
Fem – eggs (native)		Patch	24	233.10°	0.05	
		Border	22	13.80° (21.96°)	0.66**	
		1 m	24	340.01° (38.83°)	0.39*	
		3 m	21	267.57°	0.08	
Fem + eggs (native)		Patch	20	271.54°	0.18	
		Border	22	12.66° (40.83°)	0.40*	
		1 m	28	326.50° (39.01°)	0.37*	
		3 m	20	298.56°	0.14	
Males (foreign)		Patch	20	244.03°	0.25	
		Border	23	287.94°	0.14	
		1 m	18	175.13°	0.12	
		3 m	15	2.96°	0.07	
Fem – eggs (foreign)		Patch	16	70.71°	0.14	
		Border	18	359.46° (38.03°)	0.46*	
		1 m	17	358.00° (34.22°)	0.53*	
		3 m	14	261.00°	0.34	
Fem + eggs (foreign)		Patch	21	70.47°	0.15	
		Border	17	359.33° (37.67°)	0.48*	
		1 m	17	11.79° (39.21°)	0.45*	
		3 m	17	284.28°	0.18	
May	Males (native)	Patch	50	137.44°	0.16	
		Border	50	22.13°	0.13	
		1 m	44	167.56°	0.09	
		3 m	46	278.66°	0.18	
	Fem – eggs (native)	Patch	34	213.12°	0.19	
		Border	37	67.09°	0.09	
		1 m	43	110.56°	0.18	
		3 m	34	202.78°	0.14	
	June	Males (native)	Patch	40	23.23°	0.16
			Border	30	321.71°	0.11
			1 m	29	117.09°	0.22
			3 m	18	216.17°	0.19
Fem – eggs (native)		Patch	33	23.50°	0.09	
		Border	23	59.37°	0.16	
		1 m	29	138.12°	0.20	
		3 m	31	229.75°	0.11	
Fem + eggs (native)		Patch	34	67.81°	0.21	
		Border	22	276.74°	0.08	
		1 m	18	310.45°	0.15	
		3 m	30	58.08°	0.19	

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 matings under laboratory conditions (Bonte & Maelfait unpublished data). As genetic diversity in this species is not lower

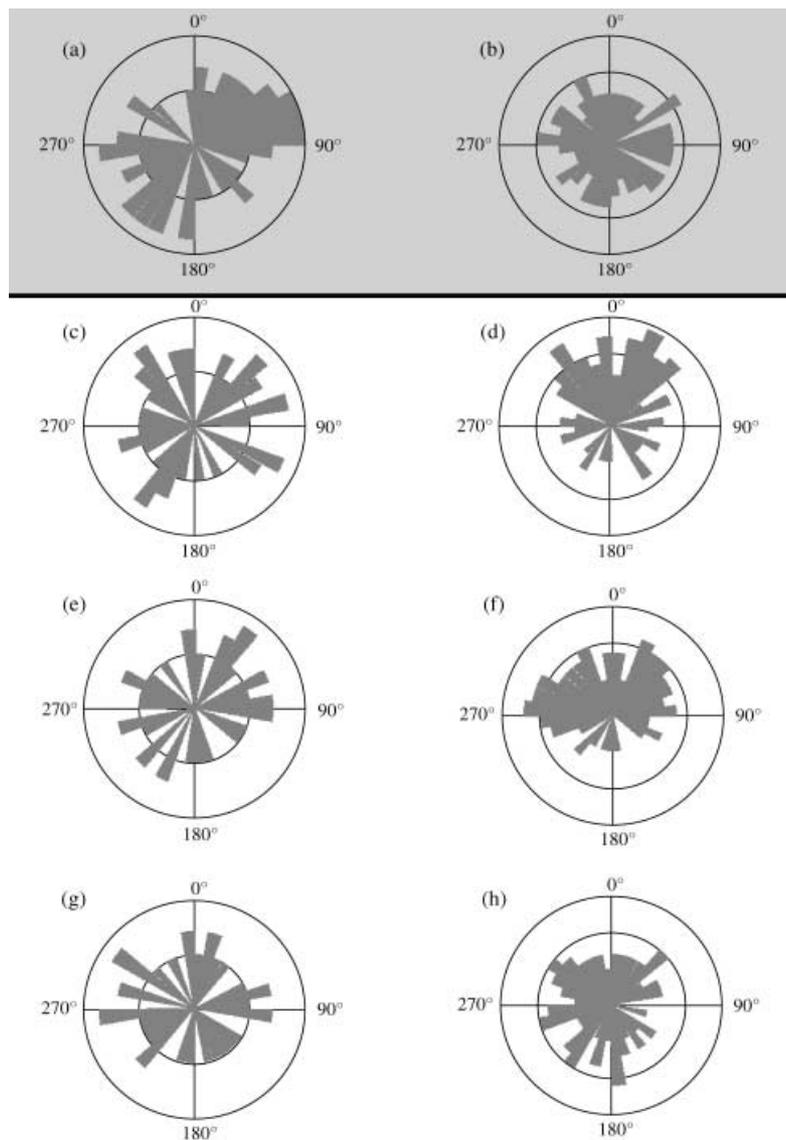


Fig. 3. Histograms depicting the results of orientation experiments for male and female *P. monticola* released at different distances from grassland patches: (a–b) at grassland centre; (c–d) at grassland edge; (e–f): at 1 m from edge; (g–h): at 3 m from edge); left panels: males, right panels: females.

in low quality patches (Bonte *et al.* 2003a), inbreeding avoidance (*sensu* Perrin & Mazalov 2000; 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 \times 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.* 2002). 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 hold only for adult males because their activity, but not that of females, is related

strongly 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 be a priori excluded 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, Roger & Thomas 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. Because adult male activity is related mainly to mate location and less so to foraging, males but not females may succeed in continuing mate-seeking behaviour across the matrix, and by so doing 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 as 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, Clutton-Brock & Grenfell 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 unpublished 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 population models. It also stresses the need for further research on the behavioural ecology of ecological landscapes (*sensu* Lima & Zollner 1996; Boudjemadi, Lecomte & Clobert 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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References

- Alderweireldt, M. & Maelfait, J.-P. (1990) Catalogus van de spinnen van België. Deel VII. Lycosidae. *Studiedocumenten Van Het KBIN*, **61**, 1–92.
- Bonte, D., Vandenbroecke, N., Lens, L. & Maelfait, J.-P. (2003b) Low ballooning propensity in habitat specialists from a fragmented landscape: rare species will become rarer. *Proceedings of the Royal Society London Series B*, **270**, 1601–1607.
- Bonte, D., Lens, L., Maelfait, J.-P., Hoffmann, M. & Kuijken, E. (2003a) Patch quality and connectivity influence spatial dynamics in a dune wolfspider. *Oecologia*, **135**, 227–235.
- 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., Van Heuverswyn, F. & Mertens, J. (2002) Temporal and spatial distribution of epigeic Arthropleona springtails (Collembola: Hexapoda) in coastal grey dunes. *Belgian Journal of Entomology*, **4**, 17–26.
- Boudjemadi, K., Lecomte, J. & Clobert, J. (1999) Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. *Journal of Animal Ecology*, **68**, 1207–1224.
- Conradt, L., Bosworth, E.J., Roper, T.J. & Thomas, C.D. (2000) Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proceedings of the Royal Society London Series B*, **267**, 1505–1510.

- Conradt, L., Roper, T.J. & Thomas, C.D. (2001) Dispersal behaviour of individuals in metapopulations of two butterflies. *Oikos*, **95**, 416–424.
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, **14**, 405–410.
- Freake, M.J. (1998) Variation in homeward orientation performance in the sleepy lizard (*Tiliqua rugosa*): effects of sex and reproductive period. *Behavioural Ecology and Sociobiology*, **43**, 339–344.
- Henschel, J.R. (2002) Long-distance wandering and mating by the dancing white lady spider (*Leucorchechestrus arenicola*) (Araneae, Sparassidae) across Namib dunes. *Journal of Arachnology*, **30**, 321–330.
- Humphreys, W.F. (1987) Behavioural temperature regulation. *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 56–65. Springer Verlag, Berlin.
- Kindvall, O., Vessby, K., Berggren, A. & Hartman, G. (1998) Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metrioptera roeseli*: an experimental study. *Oikos*, **81**, 449–457.
- Kisdi, E. (2002) Dispersal: risk spreading versus local adaptation. *American Naturalist*, **159**, 579–596.
- Kreiter, N.A. & Wise, D.H. (2001) Prey availability limits fecundity and influences the movement pattern of female fishing spiders. *Oecologia*, **127**, 417–424.
- Kuussaari, M., Sacheri, I., Camara, M. & Hanski, I. (1998) Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos*, **82**, 384–392.
- Lima, S.L. & Zollner, P.A. (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*, **11**, 131–135.
- Maelfait, J.-P. & Baert, L. (1975) Contribution to the knowledge of the arachno- and entomofauna of different wood habitats. *Biologisch Jaarboek Dodonaea*, **43**, 179–196.
- Maelfait, J.-P., Baert, L., Janssen, M. & Alderweireldt, M. (1998) A Red list for the spiders of Flanders. *Bulletin Van Het Koninklijk Belgisch Instituut Voor Natuurwetenschappen, Entomologie*, **68**, 131–142.
- Morse, D.H. (1997) Distribution, movement, and the activity patterns of an intertidal wolf spider *Pardosa lapidicina* population (Araneae, Lycosidae). *Journal of Arachnology*, **25**, 1–10.
- Morse, D.H. (2002) Orientation and movement of wolf spiders *Pardosa lapidicina* (Araneae, Lycosidae) in the intertidal zone. *Journal of Arachnology*, **30**, 601–609.
- Papi, F. (1955) Astronomische Orientierung bei der Wolfspinne *Arctosa perita* (Latr.). *Zeitschrift für Vergleichende Physiologie*, **37**, 230–233.
- Papi, F. & Syrjämäki, J. (1963) The sun-orientation rhythm of wolf spiders at different latitudes. *Archives Italiennes de Biologie*, **101**, 59–77.
- Perrin, N. & Mazalov, V. (2000) Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist*, **155**, 116–127.
- Provoost, S., Ampe, C., Bonte, D., Cosyns, E. & Hoffmann, M. (2002) Ecology, management and monitoring of dune grasslands in Flanders, Belgium. *Littoral 2002, the Changing Coast* (ed. Eurocoast), pp. 11–22. Eurocoast/EUCC, Porto, Portugal.
- Stephens, P.A. & Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution*, **14**, 401–405.
- Sutherland, W.J. (1998) The importance of behavioural studies in conservation biology. *Animal Behaviour*, **56**, 801–809.
- Thomas, C.D. & Kunin, W.E. (1999) The spatial structure of population. *Journal of Animal Ecology*, **68**, 647–657.
- Van der Aart, P.J.M. (1975) *De verspreiding van wolfspinnen in een duingebied, geanalyseerd aan de hand van multivariate technieken*. PhD thesis, Leiden University, Leiden.
- Wiebes, J.T. & Den Hollander, J. (1974) Nederlandse wolfspinnen (Lycosidae en Pisauridae). *Wetenschappelijke mededelingen. Van de Koninklijke Nederlandse Natuurhistorische Vereniging*, **44**, 1–23.
- Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall International, Inc., New Jersey.
- Zollner, P.A. & Lima, S.L. (1999) Search strategies for landscape-level interpatch movements. *Ecology*, **80**, 1019–1030.

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