Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider

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Dispersal can be regarded as a process operating both between and within patches of suitable habitat. For uncontrolled dispersal processes, the risk of crossing the borders of the habitat patch and arriving in the unsuitable landscape matrix will increase with decreasing patch area, in particular when the distance between isolated habitat patches is larger than the species’ average dispersal capacity. Ballooning dispersal in spiders can be considered as a passive dispersal process, in which dispersed distances depend on the prevalent wind velocity. We executed a reaction norm analysis to analyze how dispersal propensity of the salt marsh wolf spider *Pardosa purbeckensis* depended on population characteristics (patch size) and the environment (wind velocity). Dispersal propensity was affected by the interaction between wind velocity and maternal patch size. Ballooning propensities decreased with decreasing salt marsh size. Interestingly, genotypes from large salt marshes show higher ballooning propensities under higher wind velocities, whereas those from small habitat patches show their highest dispersal propensity under low wind velocities. Crossing reaction norms and subsequently strong genotype × environment interaction variation was observed in all populations but tended to be lower in genotypes from large salt marshes. It is likely that this pattern results from differences in wind velocity–related costs of within-habitat dispersal in salt marshes of different sizes. *Key words*: ballooning, behavioral plasticity, Lycosidae, *Pardosa purbeckensis*, reaction norm. [Behav Ecol 18:438–443 (2007)]

Theoretical and empirical studies suggest that dispersal, that is, one-way movements to breeding locations away from the place of birth (Dingle 1996), is favored by natural selection through kin competition, inbreeding avoidance, and temporal variability in habitat quality, and counterselected by a high level of spatial environmental heterogeneity and niche specialization (reviews in Clobert et al. 2001; Bullock et al. 2002). Dispersal is often considered at the landscape level, that is, as movements between patches of suitable habitat. When these patches become so isolated that between-habitat dispersal is seriously hampered, selection against dispersal can be expected. However, in case the species occurs in aggregated, discrete microhabitats, dispersal implies also within-habitat movements for which dispersal may remain evolutionary beneficial, despite large distances between the habitat patches. The nature of the dispersal process involved, that is, active dispersal with control versus passive uncontrolled dispersal, may influence the outcome of selection processes (Bonte et al. 2006) in interaction with area and connectivity of the habitat patch. In case of controlled dispersal, costs of within-habitat dispersal are intrinsically equal for habitats of different sizes, whereas for uncontrolled dispersal processes, the risk of crossing the borders of the habitat patch and arriving in the unsuitable landscape matrix will increase with decreasing patch area or increased habitat specialization (Bonte et al. 2003).

In contrast to predator-imposed escape behavior (e.g., Plaistow and Siva-Jothy 1999; Relyea 2004; Laurila et al. 2006; Wohlfahrt et al. 2006), between-population variation in plasticity of dispersal behavior is currently hardly addressed. For spiders characterized by passive dispersal (ballooning), the length of the dispersal path is determined to a large extent by environmental factors related to landscape structure, such as the spatial configuration of “obstacles” and wind velocity (Bell et al. 2005), with higher velocities resulting in longer dispersal events (Thomas et al. 2003). Consequently, the probability of reaching suitable habitat is unpredictable at the moment an individual decides to disperse because it depends on intrinsically unpredictable wind currents. According to Thomas et al. (2003), single flight dispersal distances equal on average 978 m but may reach 3000 m and more under wind velocities of 1.75 m s\(^{-1}\). In contrast to smaller species, ballooning of larger wolf spiders is restricted to periods in which spiderlings have optimal mass and size, that is, during the second or third instar (Richter 1970, 1971). This period takes only 2 or 3 weeks and its starting time largely depends on the timing of egg sac production and hatching.

Ballooning is characterized by stereotypic behavioral adaptations, referred to as tiptoe behavior (e.g., Weyman et al. 2002; Bell et al. 2005). As any other behavioral trait, it can be expected to show phenotypic plasticity (West-Eberhard 1989; Pigliucci 2001). Adaptive behavioral plasticity (i.e., in which the behavioral plasticity is beneficial; Gotthard and Nylin 1995) is expected to evolve more readily than adaptive morphological plasticity because there are more potential cues within the environment (West-Eberhard 1989), and changes in behavior will become effective in a shorter time period. Because different attributes of behavioral plasticity (e.g., height and slope of the reaction norm) may evolve independently (e.g., Schlichting and Levin 1986), only comparative analysis of behavioral plasticity (e.g., Burghardt and Krause 1999; Van Buskirk 2002; Bell and Stamps 2004) will allow insight into microevolutionary mechanisms in spatially structured populations (Relyea 2002). For instance, an equal average phenotypic trait over all genotypes in different environments may either result from the combined effect of genetic invariability and canalization (i.e., the phenotype is independent of environmental variation—a flat reaction norm and the absence of plasticity and of genetic variation in plasticity) or from the antagonistic genetic variation in...
plasticity (i.e., genotypes have crossing reaction norms). Assessment of this distinction is important in the context of evolutionary conservation because absence of plasticity implies low resilience toward changing environmental conditions (Via and Lande 1987; Gillespie and Turelli 1989).

Here, we report the results of an experiment testing for patterns in individual dispersal propensity and its plasticity toward 2 wind velocities for a highly stenotypic salt marsh wolf spider from several highly isolated populations. Assuming that wind velocity–related and area-related costs differ between spiderlings of salt marshes from different size, we predict 1) that ballooning frequency will increase with increasing patch size under both low and high wind velocities, with a stronger canalization toward low dispersal propensity in small populations, 2) a more pronounced increase in dispersal propensity under high wind velocities, and 3) that higher spatial heterogeneity within larger salt marshes will result in a stronger genotype × environment interaction.

**MATERIALS AND METHODS**

**Females of the species and populations**

**Pardosa purbeckensis** (F.O. Pickard-Cambridge 1895) is the most dominant wolf spider species in European coastal salt marshes (Baert and Maelfait 1999; Pettillon et al. 2004). The species has an annual–biennial life cycle with reproduction in May–June. Egg sacs are attached to spinnerets of wandering females and hatch from June onward to August. Females carrying egg sacs were sampled in 7, strongly isolated populations along the coastline between Normandy (Mont Saint Michel) and the Netherlands (Zwin); see Figure 1. These salt marshes differ in age and area of suitable habitat (Table 1), which are significantly positively correlated ($R = 0.88; P < 0.05$). Earlier population genetic analyses through allozymes indicated low genetic differentiation among populations and no differences in genetic diversity within populations (Maelfait J.-P, Hendrickx F, unpublished data). Offspring were individually reared under standardized temperature ($20 ± 2\, ^{\circ}\text{C}$) and 16:8 h day/night regimes and fed ad libidum with *Sinella curviseta* springtails until they reached the second postnatal instar. Because all spiderlings hatched in the laboratory, they had not experienced their natal environment.

**Figure 1**

Location of the sampled population. 1, Baie de Mont Saint Michel; 2, Baie de la Somme; 3, Baie de la Canche; 4, Ambleteuse; 5, Nieuwpoort; 6, Baai van Heist; and 7, Zwin.

**Table 1**

Overview of the sampled salt marshes with estimated age, area of suitable habitat (Natura 2000 fiches des sites—http://natura2000.environnement.gouv.fr/habitats/HAB1130.html—AMINAL, personal communication), number of sampled females, and number of tested spiderlings

<table>
<thead>
<tr>
<th>Site</th>
<th>Age (years)</th>
<th>Area (hectares)</th>
<th>$N_{\text{females}}$</th>
<th>$N_{\text{spiderlings}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baie de Mont Saint Michel</td>
<td>7000</td>
<td>1937</td>
<td>11</td>
<td>208</td>
</tr>
<tr>
<td>Baie de la Somme</td>
<td>2500</td>
<td>1567</td>
<td>10</td>
<td>222</td>
</tr>
<tr>
<td>Baie de la Canche</td>
<td>2500</td>
<td>80</td>
<td>11</td>
<td>154</td>
</tr>
<tr>
<td>Ambleteuse—Le Slack</td>
<td>1000</td>
<td>5</td>
<td>6</td>
<td>175</td>
</tr>
<tr>
<td>Nieuwpoort—Bjernmonding</td>
<td>900</td>
<td>4</td>
<td>6</td>
<td>135</td>
</tr>
<tr>
<td>Baai van Heist</td>
<td>10</td>
<td>1</td>
<td>7</td>
<td>125</td>
</tr>
<tr>
<td>Knokke—Zwin</td>
<td>700</td>
<td>60</td>
<td>9</td>
<td>248</td>
</tr>
</tbody>
</table>

Assessment of aerial dispersal propensity

Ballooning behavior of *P. purbeckensis* was quantified under standardized laboratory conditions. Groups of 5 individuals originating from the same mother were placed on a platform, of which escaping was prevented by a vertical border. On the platform, mosses were provided as shelter and ballooning was possible by climbing on vertical screws. A mesh was placed 5 cm above the platform, enabling attachment of the produced silk threads. Only ballooning spiderlings could get attached to this mesh. After 30 min testing, all attached spiderlings were collected. Two similar experimental setups were used with upward current of 0.3 and 0.8 m s$^{-1}$, temperature of 30 $^{\circ}\text{C}$, and relative aerial humidity of 40–50%, respectively. These wind velocities were chosen because preliminary tests indicated that species from all populations engage in ballooning dispersal under these velocities, whereas much lower frequencies were recorded at velocities higher than 1.2 m s$^{-1}$ (Bonte D, unpublished data). Given the binomial distribution of the analyses (see further), sufficient variation (and power) is consequently guaranteed.

A total of 1342 spiderlings, originating from 60 clutches were tested. Neither maternal size ($F_{0,54} = 1.61; P = 0.163$) nor clutch size ($F_{6,33} = 0.19; P = 0.977$) differed between the sampled populations.

**Statistical analysis**

The observed ballooning probabilities $b$ of spiderlings from clutch $i$, location (area) $j$, under wind velocity $k$ was modeled using the following binomial mixed model:

$$\text{Logit}(b_{ijk}) = \mu + a_i + w_j + (aw)_{ijk} + g_k + (gw)_{ijk} + e_{ijk},$$

where $\mu$ = grand mean, $a_i$, $w_j$, $(aw)_{ijk}$ are effects of location, wind velocity, and interactions, and $g_k$, $(gw)_{ijk}$ are variance components of genotype (clutch), genotype-by-wind ($G \times E$), and residuals, respectively. Analyses were conducted for 7 populations, 2 wind velocities (0.3 and 0.8 m s$^{-1}$), and 60 genotypes by Bayesian estimation using a Monte-Carlo Markov chain (MCMC) procedure in WinBugs v 1.4. (Spiegelhalter et al. 2003). Within this regression model (Equation 1), the following parameter posterior distributions were estimated: intercept $\alpha_0$, slope patch area $\alpha_{\text{area}}$ effect wind velocity $\alpha_{\text{wind}}$, slope interaction wind velocity × patch area $\alpha_{\text{windarea}}$; Variance due to clutch varG and variance due to clutch × wind interaction varGE. In a second model, varGE estimates (1000 random samples from MCMC permutation) for each of the 7 populations were regressed on patch area in order to assess the distribution of the estimated posterior regression slopes between genotype × environment interaction variance and...
patch area of the population of origin. In the latter, posterior distributions of the intercept \((b_0)\) and the regression slope \((b_1)\) were estimated. Area of the salt marshes was \(\log_{10}\) transformed.

Flat priors for regression coefficients were drawn from a normal distribution with a mean of 0 and a standard deviation (SD) of 1000 because we did not have any a priori knowledge on parameter distributions. Priors for variance components were drawn from a positively constraint uniform distribution with a mean of 0 and SD 1. To assure accurate MCMC simulations from the prior distributions, an initial “burn in” of 10 000 iterations was performed and discarded from analysis. This was followed by 1 00 000 iterations for both analyses. After visual inspections for possible autocorrelation and assessing chain convergence (Brooks-Gelman-Rubin diagnostics; Brooks and Gelman 1998), the mean and SD of each parameter (regression coefficients and variance estimates) were calculated, as were the 2.5th and 97.5th percentiles of the sample. These were used to describe the 95% Bayesian credible interval. The mean and SD of the posterior distributions of the parameters were used to assess effects of each of the variables.

RESULTS

Effects of wind velocity and area of the maternal habitat

We were not able to assess directly the main effects of wind velocity and the area of the maternal salt marsh on the probability of ballooning because both show a strong interaction (Table 2). Ballooning probabilities within clutches are lower in populations from small salt marshes compared with those from the larger salt marshes (on average 10% in the smallest areas up to on average 30% in the largest ones; Figure 2). As expected, ballooning probabilities show a steeper increase with increasing marsh size at the highest wind speed. This means that habitat loss negatively affects dispersal probabilities and that this effect is more pronounced under higher wind velocities. This lower dispersal probability was however not accompanied by a loss of genetic variation in interaction variation within each of the 7 populations (Figure 3). G \( \times \) E variation shows a tendency (slope = \(-0.072 \pm 0.002\) SD; Table 2) to be lower in very large habitats. Reaction norms are indeed proportionally more parallel in clutches from larger habitat (Figure 4). Consequently, higher observed phenotypic similarity under both wind velocities in genotypes from small areas does not originate from flat reaction norms, but rather from crossing reaction norms, as indicated by the large estimated G \( \times \) E variation in these populations.

DISCUSSION

The results indicate that the probability of the onset of passive dispersal (ballooning) for a salt marsh wolf spider depended on the interaction between factors related to the population (patch size) and the strength of the transporting medium (wind velocity). As expected, ballooning probabilities showed a steeper increase with increasing marsh size at the highest wind speed. This means that habitat loss negatively affects dispersal probabilities and that this effect is more pronounced under higher wind velocities. This lower dispersal probability was however not accompanied by a loss of genetic variation in

<table>
<thead>
<tr>
<th>Effect</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>Median</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-2.890</td>
<td>0.582</td>
<td>-3.972</td>
<td>-2.856</td>
<td>-2.292</td>
</tr>
<tr>
<td>Area</td>
<td>0.470</td>
<td>0.255</td>
<td>0.033</td>
<td>0.472</td>
<td>0.961</td>
</tr>
<tr>
<td>Wind velocity</td>
<td>1.201</td>
<td>0.377</td>
<td>0.451</td>
<td>1.209</td>
<td>1.93</td>
</tr>
<tr>
<td>Area ( \times ) wind velocity interaction</td>
<td>-0.637</td>
<td>0.159</td>
<td>-0.955</td>
<td>-0.640</td>
<td>-0.323</td>
</tr>
<tr>
<td>Genotype</td>
<td>0.490</td>
<td>0.234</td>
<td>0.117</td>
<td>0.461</td>
<td>1.036</td>
</tr>
<tr>
<td>Genotype ( \times ) environment</td>
<td>0.279</td>
<td>0.165</td>
<td>0.042</td>
<td>0.251</td>
<td>0.678</td>
</tr>
</tbody>
</table>

Table 2

Mean (and SDs) and median values (and 95% Bayesian credibility interval) of 1) posterior distributions of parameters for the binomial regression model of spiderling ballooning probability in relation to wind velocity and area of the maternal habitat and 2) posterior distributions of parameters for the regression model of genotype \( \times \) environment variation within each population and area of the maternal habitat.

Figure 2

Effects of maternal salt marsh area and wind velocity (full line: 0.3 m s\(^{-1}\); dashed line: 0.8 m s\(^{-1}\)) on the ballooning probability of *Pardosa purbeckensis* spiderlings. Dots indicate average observed frequencies for a given clutch and lines indicate statistical inferred probabilities.
plasticity, but rather related to a higher amount of crossing reaction norms. Because age and area of the several populations were positively correlated in our study, we can conclude that founder effects (Descendorf et al. 1998; Hanski et al. 2004) are not responsible for the observed variation in ballooning behavior and plasticity.

Dispersal behavior and reaction norms

This study differs from other reaction norms approaches related to environmental gradients (e.g., stress: Kohler et al. [2000], prey availability: Burghardt and Krause [1999], or predator regime: Van Buskirk [2002]) in a sense that the environmental variation was not imposed during a long term on organisms during development. Instead, we studied short-term plasticity in behavior toward rapidly changing environmental factors and used reaction norm analysis to assess responses of different genotypes. This resulted in a strong among-genotype variation of dispersal behavior in relation to the prevailing wind speed. In the majority of studies on dispersal plasticity, strong context dependence dispersal behavior is detected, predominantly, because the individuals experienced differences in habitat structure or quality (Van Dyck and Baguette 2005), rather than due to genetic factors. In our setup, however, spiderlings are reared in the laboratory from wild-caught females, so that an effect of experience with the native habitat can be excluded. Moreover, the environment differed only in one factor (i.e., wind velocity). Consequently, the observed dispersal plasticity is most likely to be caused by genetic or maternal factors (genotype or population of origin) and may potentially reflect adaptive (i.e., beneficial) patterns through selection or maternal effects.

Adaptive plasticity

The observed patterns in reaction norms corresponded to what was expected with respect to differences in dispersal costs between small and large populations. This indicates that ballooning dispersal propensity as a behavioral plastic trait is adaptive, that is, beneficial under local conditions (Gotthard and Nylin 1995). This adaptive plasticity may be the result of ultimate (evolutionary) factors as well as of proximate maternal effects. Although no differences in female size (related to spiderling size; Bonte et al. 2006), clutch size, or sex-ratio distortion (with possible gender-related dispersal; Ims 1990) during controlled breeding (Bonte D, unpublished data) were observed, maternal effects cannot be completely excluded (Ims and Hjermann 2001; Bowler and Benton 2005) because, for example, hormonal differences may have caused similarity among siblings (Massot and Clobert 2000).

Ultimate selection pressures on dispersal traits but habitat area (i.e., temporal and spatial variability in habitat quality, avoidance of competition; Bowler and Benton 2005) can be assumed to be similar in all salt marshes. The underlying mechanism to explain the observed patterns in dispersal plasticity is hence most likely selection against dispersal in small populations. Despite evolutionary benefits of within-habitat dispersal in naturally disturbed environments (Southwood 1962), ballooning may be hampered by the large distances between coastal salt marshes, whereby multiple takeoffs are hardly possible due to the hostile matrix. This means that the risk of arriving in the nonsuitable matrix after within-habitat dispersal is probably too high for individuals from small salt marshes, in particular when wind velocity is high. Ballooning propensities of genotypes from small areas are indeed observed to be lower under high wind velocity than under low wind velocity, indicating the high dispersal costs under these conditions.

For this reason, dispersal patterns may be shaped by an increased cost of within-habitat movements, rather than by costs of interhabitat dispersal (Bonte et al. 2006). This implies that a decreased probability of dispersal behavior is related to the reduction in area of suitable habitat, as has been shown in wind-dispersed plants of inshore islands (Cody and Overton 1996). Additionally, lower ballooning probabilities under low wind velocities for genotypes from larger salt marshes suggest low benefits of short aerial trajectories. As recently shown for a related wolf spider, similar short distances can be covered by hitchhiking dispersal (i.e., transportation by the mother; Bonte et al. forthcoming), with lower risks due to trajectory control abilities (Morse 2002; Bonte et al. 2004; Krauss and Morse 2005).

Loss of plasticity at the population-level but not its genetic variation

Variation in reaction norms is a prerequisite to maintain genetic variation in spatially or temporally heterogeneous environments with overlapping generations (Via and Lande 1987; Gillespie and Turelli 1989) and assures sufficient resilience toward changing environmental conditions. We found that ballooning plasticity in all investigated populations was accompanied by variation in plasticity (G × E interactions), indicating the presence of genetic variation (Via et al. 1995). Moreover, populations from small salt marshes seemed to show increased variation due to antagonistic crossings of reaction norms. As evidenced by van Kleunen and Fisher (2001), genetic variation in plasticity can be maintained on small spatial scales of only a few meters (Stratton 1994; van Kleunen and Fisher 2001). Temporal variation in weather conditions, including wind velocity, can here be assumed to maintain dispersal plasticity because spiderlings from different genotypes differ in the timing of dispersal events due to variation in the time window of hatching and juvenile development. Therefore, maladaptive reaction norms in small salt marshes (i.e., genotypes promoting dispersal under high wind velocities) may only be counterselected during periods of high wind velocities but not during periods of low wind velocities. In contrast, these behavioral types can be expected to be favored in populations from large areas in disadvantage of the genotypes not promoting dispersal under high wind velocities.
Figure 4
Reaction norms for ballooning propensity within clutches over the 2 studied wind velocity environments from spider originating from the 7 populations. Dots indicate average observed frequencies for a given clutch. (A) Baai van Heist, (B) Nieuwpoort, (C) Ambleteuse, (D) Zwin, (E) Canche, (F) Somme, and (G) Mont Saint Michel.
This may result in more uniform reaction norms, which was confirmed by the lower observed variation in plasticity.

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