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Heritability of spider ballooning motivation under different wind velocities

Dries Bonte* and Luc Lens

Terrestrial Ecology Unit, Department of Biology, Ghent University,
K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium

ABSTRACT

Background: Ballooning is the main dispersal mode in small spiders, by which individuals are carried by wind currents as spheres attached to thin silk threads. It involves a typical and unique pre-dispersal 'tiptoe' behaviour that can easily be observed under laboratory conditions.

Hypotheses: Is the ballooning behaviour of a saltmarsh-inhabiting spider heritable? Do heritability estimates differ under two different environmental conditions (wind velocity)?

Organism: Second-instar offspring from *Pardosa purbeckensis* (Lycosidae; Araneae).

Site of experiments: Parents were collected in a large and a small saltmarsh. Offspring were tested for behavioural variation under standardized laboratory experiments.

Methods: Ballooning motivation (tiptoe behaviour) was assessed at two wind velocities in wind tunnels. We conducted a quantitative (half-sib) genetic analysis of ballooning motivation and applied threshold models to estimate heritabilities under both wind conditions.

Results: Heritability estimates were 0.17 (standard error = 0.07) at low wind velocities and 0.42 (standard error = 0.21) at high wind velocities. Because of the absence of a genetic correlation among the two wind environments, independent selection on dispersal motivation under different wind velocities must be prevalent.

Keywords: dispersal, *Pardosa*, saltmarsh, selection, threshold model.

INTRODUCTION

Behavioural ecology is heavily influenced by evolutionary thinking, but quantitative genetic approaches that aim to detect additive variation are generally ignored (Owens, 2006). The understanding of differences between phenotypic and genetic patterns may be especially crucial when behavioural variation is directly related to fitness. Although Owens (2006) did not focus on dispersal behaviour in particular, movement behaviour in its widest sense is assumed to be related to fitness, especially in cases where dispersal occurs in a semi-passive way with direct mortality costs due to landscape-related factors (Bonte *et al.*, 2003). More specifically, selection pressures due to habitat fragmentation may strongly shape dispersal

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* Author to whom all correspondence should be addressed. e-mail: dries.bonte@ugent.be

behaviour in passive dispersers because dispersal trajectories will depend entirely on the specific properties of the transporting medium (Bonte *et al.*, 2006; Drew and Eggleston, 2006). For arthropod species that passively disperse through wind currents, such as ballooning spiders, mites, and caterpillars (Bell *et al.*, 2005), dispersal trajectories will largely depend on physical drag properties (i.e. vertical and horizontal directionality, strength) of the currents, whereas individual morphology (body posture, mass) and length of the silk threads (if necessary to generate sufficient drag) appear to influence flight trajectories only in a marginal and negligible way (Bell *et al.*, 2005; Reynolds *et al.*, 2006). Consequently, when habitat becomes fragmented and reduced, costs of dispersal can be expected to be much higher for passive than active dispersers with certain flight control (With *et al.*, 1997; Bonte *et al.*, 2006).

To date, geographic and micro-evolutionary determined variation in dispersal behaviour or dispersal-related morphological traits has been observed in a variety of arthropod taxa (e.g. Gatehouse, 1997; Desender *et al.*, 1998; Hanski *et al.*, 2004). Given the widely acknowledged landscape-related and conditional-dependent phenotypic pathways (Clobert *et al.*, 2001), only a few attempts have been made to distinguish environmental from additive genetic components (e.g. Dingle, 1968; Desender, 1989; Li and Margolies, 1993, 1994). Environmental and genetic effects should not act mutually exclusively on the phenotype. As shown by Leimar *et al.* (2006), morph determination can sometimes be regarded as adaptive developmental plasticity, in which the phenotype is determined through combined environmental and genetic factors, which should appear as genetic variation in reaction norms. In these cases, additive variation should be prevalent under different environmental conditions, but genetic correlations among environments should be absent (Relyea, 2005). Hence, selection can act under different environments in independent ways.

Heritability of behaviour is generally found to be similar to that of life-history traits, but lower than that of morphological traits (Stirling *et al.*, 2002). Falconer (1989) argued that the connection between the nature of a character and the magnitude of heritability is related to the trait's relationship with fitness, with those least connected to fitness having the highest heritabilities [Fisher's fundamental theorem (Merilä and Sheldon, 1999)]. Similarly, highly integrated behaviours (those that integrate a high number of other component behaviours) are presumed to show lower heritabilities because they are more closely linked to fitness than less integrated behaviours (Stirling *et al.*, 2002). In general, (broad-sense) heritability estimates of invertebrate behavioural characters are estimated to be 0.30 (standard error = 0.02), with the lowest heritabilities for behaviours related to foraging and movement (Stirling *et al.*, 2002).

Spiders engage in aerial dispersal through ballooning (Weyman, 1993; Weyman *et al.*, 2002). This behaviour is typically subject to individual decision-making as a reaction towards wind velocity (Weyman *et al.*, 2002). The onset-decision and the length of the dispersal trajectory (dispersal ability) are consequently largely determined by wind velocity (Bell *et al.*, 2005), with higher velocities resulting in longer dispersal trajectories (Thomas *et al.*, 2003), and variation in dispersal motivation (Richter, 1970; Vugts and van Wingerden, 1976). Despite the fact that individuals may have the ability to adapt their terminal velocity by changing postures (Suter, 1992) or thread lengths (Bell *et al.*, 2005), the uncertainty of reaching suitable habitat is high at the moment an individual makes the decision to disperse because the nature of wind currents remains intrinsically unpredictable. Based on theoretical models (Thomas, 1996; Thomas *et al.*, 2003), the length of single dispersal trajectories can be estimated to vary between 150 and 400 m at wind velocities of 1.5–2.9 $m \cdot s^{-1}$, with more than 40% of individuals eventually travelling distances more than 500 m. At wind velocities of 0.8–1.0 $m \cdot s^{-1}$, distance travelled will approximate on average 100 m, with more than 40% of aerial dispersers covering distances of 250–300 m. Consequently, the risk of landing in hostile habitat is extremely high at high wind velocities. Even at low wind velocities, direct mortality after dispersal in small isolated habitat remnants of less than 5 ha can be expected for most of the ballooners.

As earlier studies revealed significant population-wide reductions in ballooning motivation after habitat fragmentation and habitat loss (Bonte *et al.*, 2006, 2007) in accordance with expectations of selection, genetic variance in this plastic trait and its reaction norm is expected at different wind velocities. Because unfavourable environmental conditions may have consistent effects on the expression of genetic variation through heritability estimates (Hoffmann and Merilä, 1999), we examine whether the heritability of dispersal will change under such unfavourable conditions (high wind velocities), bearing in mind the possibility of an increase in heritability due to stronger behavioural canalization towards lower dispersal motivation at high wind velocities. This is, however, only one of the plausible responses of heritability responses towards stress. As reviewed by Hoffmann and Merilä (1999), genetic variation of a trait and its heritability show unpredictable directions under unfavourable conditions, due to the prevalence of various genetic mechanisms within the selection history. Because stipulated 'generalizations' are mainly based on classical model systems (Kellermann *et al.*, 2006), and may not generalize to restricted species (Owens, 2006), especially in wild populations (Charmantier and Garant, 2005), our aim is not to test one hypothesis explicitly; rather, we provide data on the prevalence of stress-induced changes in heritability of a behavioural trait under temporally, instead of spatially, varying environmental conditions.

METHODS

Study species and breeding design

Pardosa purbeckensis F.O. Pickard-Cambridge 1895 is, numerically, the most dominant wolf spider species in coastal saltmarshes (Baert and Maelfait, 1999; Pétillon *et al.*, 2004), showing well-developed osmoregulatory adaptations. This wolf spider has an annual–biennial life cycle with reproduction in May–June. Egg sacs are attached to spinnerets of wandering females and hatch between June and August. Like *P. monticola* (Bonte *et al.*, 2006), *P. purbeckensis* shows significant within-clutch and within-population variation in dispersal motivation, with higher propensities in large, continuous habitat (Bonte *et al.*, 2007).

We collected sub-adult males and females at the beginning of May 2006 from two strongly isolated populations along the North Sea coast of France (Dept. Nord-Pas-de-Calais): the small saltmarsh of Ambleteuse (6 ha) and a larger one near Le Touquet (Baie de la Canche; 80 ha). These spiders were reared to maturity under standardized laboratory conditions (20°C, 16 h/8 h day/night regime, and relative humidity ~80%) in individual containers with an excess of prey (fruitflies). Males of both populations were randomly mated with two females to obtain a half-sib design. This allowed us to estimate narrow-sense heritability of the trait in question (Lynch and Walsh, 1998). Offspring were subsequently individually reared under standardized conditions (temperature of 20 ± 2°C and 16 h/8 h day/night regime) and fed *ad libidum* with *Sinella curviseta* springtails until they reached the second post-natal instar. These instars show the highest ballooning motivation (Richter, 1970) and were consequently used for behavioural experiments. Because all spiderlings hatched into the lab, they had no direct prior experience with their natal environment. In total, we were able to obtain 796 half-sibs from 17 males and 34 females.

Assessment of aerial dispersal propensity

Ballooning is characterized by stereotypic behavioural adaptations, known as ‘tiptoe’ behaviour: spiders position themselves at an elevated starting point, stretch their legs, raise their abdomen, and finally produce long silk threads that carry them up in the air currents. The individual prevalence of ballooning behaviour of *P. purbeckensis* was quantified under standardized laboratory conditions. Groups of five individuals, originating from the same mother, were placed on a platform in which escape was prevented by a vertical border. On the platform, mosses were provided as shelter and ballooning was possible by climbing on vertical screws (7 cm). Five centimetres above these screws, we installed a mesh (1 mm^2 mesh width) that enabled the attachment of the produced silk threads. A fan created upward wind currents. Only tiptoeing spiderlings became attached to this mesh and escaped by this means. After 30 min testing, all escaped spiderlings were collected. Siblings from 28 half-sib families were tested in the wind tunnel at a wind velocity of 0.3 or 0.8 $m \cdot s^{-1}$, temperature of 30°C, and relative aerial humidity of 40–50%. Spiderlings from another three half-sib families were only tested at the higher wind velocity because of limited clutch size ($n < 10$). Consequently, the expression of ballooning behaviour of 28 half-sib families could be assessed under two wind velocities, and tested for genetic correlations. These wind velocities were chosen *a priori* because preliminary tests and literature indicated that species from all populations engage in ballooning dispersal at these velocities, while much lower frequencies (with loss of any within- and between-clutch variation) were recorded at velocities >1.5 $m \cdot s^{-1}$ (Richter, 1970; D. Bonte *et al.*, unpublished data). Given the binomial distribution of the analyses (see below), sufficient variation (and power) is consequently guaranteed.

Data analysis

Differences in ballooning frequencies within clutches according to the four different crossing types were assessed through generalized binomial models with population of males, population of females, and wind velocity as independent variables. A binomial data distribution was modelled through logit-link transformations (Procedure Glimmix; SAS statistical package version 9.1, SAS 2003). Effective degrees of freedom were estimated by the Satterthwaite procedure to correct for the unbalanced design. Variance due to sire and dam effects (within sires) were estimated by treating them as random variables. A backward procedure was applied to reduce the full model.

The number of tiptoe-performing spiderlings n_i within a clutch N_i follows a binomial distribution. Consequently, genetic parameters cannot be estimated by variance analyses based on likelihood or least-square methods, instead threshold models need to be applied (Roff, 1997, 2001; Bégin and Roff, 2002). The threshold method posits that the determination of dimorphic variation is a consequence of the underlying liability, that is itself continuously distributed and that estimates according to threshold algorithms provide unbiased estimates of heritability. Therefore, we divided our data on within-clutch ballooning proportions (probabilities) at the median and estimated heritabilities on the 0/1 scale ($h^2_{0,1}$), using the same design for half-sib analyses as for continuous data (Roff, 1997). Standard errors were estimated by the approximate formula for unequal family sizes developed by Swiger, Harvey, Everson, and Gregory (Roff, 1997, p. 42). To obtain the corresponding estimates on the liability scale of threshold traits, both heritabilities and standard errors were transformed using the formula developed by Dempster and Lerner (1950), which corrects for the observed frequencies (Roff, 2001). Heritabilities and their standard errors given in this paper correspond to the liability, not the 0/1 scale. Genetic correlations of ballooning behaviours between the two environments (wind velocities) were estimated using covariances on 0/1 data from a mixed-model analysis of variance (Fry, 1992; Roff, 2001; Roff and Gélinas, 2003).

RESULTS

The observed ballooning motivation showed large within-sire and within-dam variation (Fig. 1). Mean ballooning propensity at a wind velocity of 0.3 $m \cdot s^{-1}$ was 25.5% (range 0–50%) and that at a wind velocity of 0.8 $m \cdot s^{-1}$ was 33.6% (0–82%).

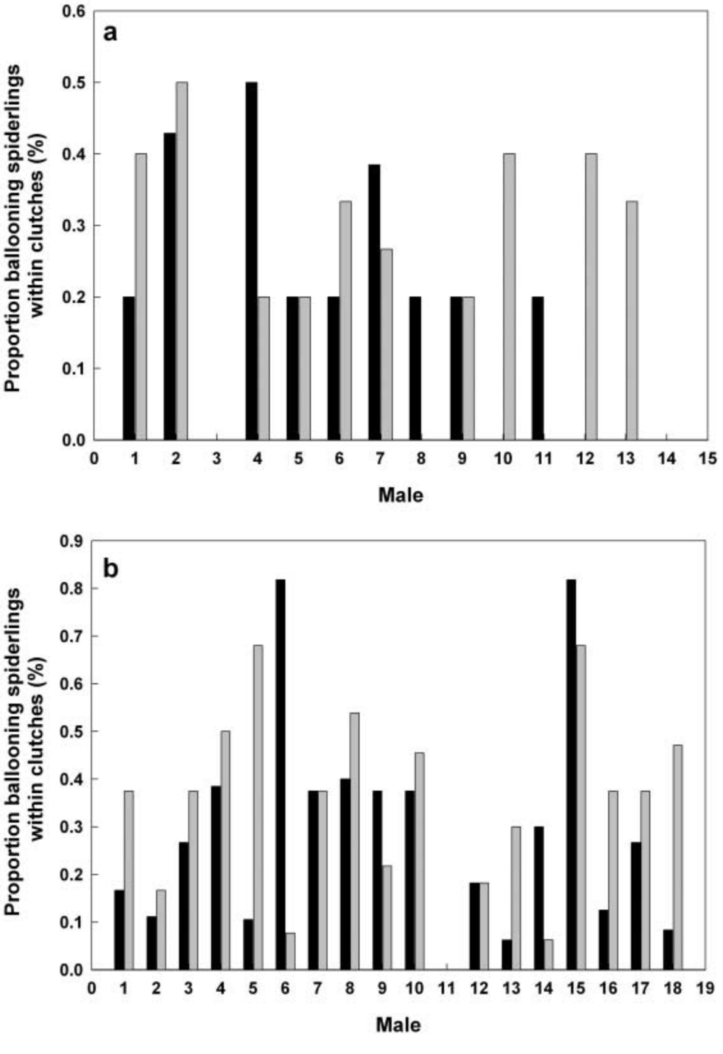

Fig. 1. Observed frequencies of ballooning spiderlings within two females (pairs of black and grey bars), mated to one male (numbered on the x-axis), at wind speeds of 0.3 $m \cdot s^{-1}$ (a) and 0.8 $m \cdot s^{-1}$ (b) respectively.

When crossings between sires and dams from the two populations were taken into account, ballooning probability differed according to the population of origin of the sire in interaction with wind velocity (Table 1). This interaction is reflected in crossing reaction norms in relation to wind velocity (Fig. 2). Variation due to sire and

Table 1. Results of the generalized mixed logistic model for ballooning propensity within clutches in relation to the sire (PopSire) and dam (PopDam) population of origin and wind velocity (wind)

Fixed effect	Numerator d.f.	Denominator d.f.	*F*-value	*P*
PopSire	1	11.48	0.09	0.771
PopDam	1	21.32	0.23	0.636
Wind	1	7.98	0.02	0.886
PopSire × PopDam	1	19.99	0.29	0.603
PopSire × Wind	1	7.986	5.73	0.044
PopDam × Wind	1	27.88	1.90	0.178
PopSire × PopDam × Wind	2	22.78	0.12	0.889
Random effect	s^2	S.E.		
Dam(Sire)	0.095	0.077		
Sire	0.734	0.377		
Dam(Sire) × Wind	0.001	0.000		
Sire × Wind	0.137	0.120		
Residual	0.427	0.128		

Note: Sire and dam(sire) variation was estimated through random effects. S.E. = standard error.

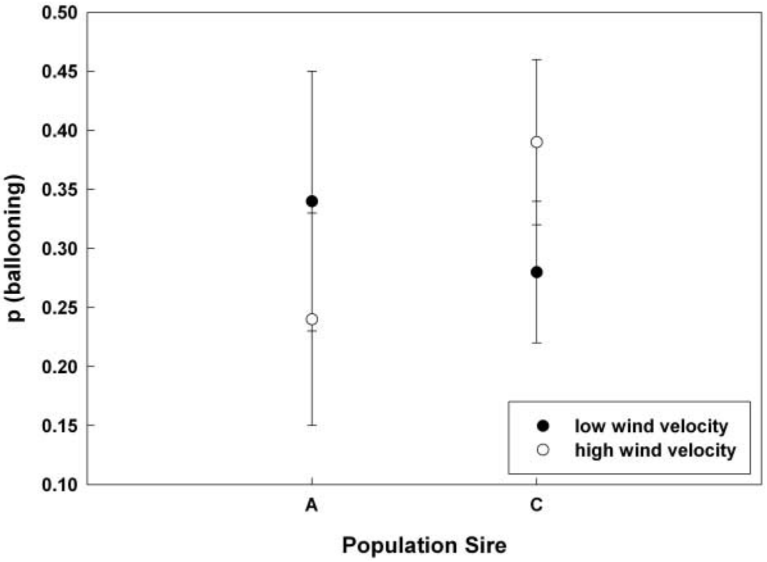

Fig. 2. Average proportion of ballooning spiderlings within clutches in relation to the sire's population of origin (A = small saltmarsh Ambleteuse; C = large saltmarch Baie de la Canche) and wind speed (low = 0.3 m · s^{-1}; high = 0.8 m · s^{-1}).

sire × wind velocity are substantial (Table 1). Sire variation is substantially larger than zero at low (mean ± standard error: 1.08 ± 0.56) and high wind velocities (0.81 ± 0.38) and reflect the presence of additive variation under the two environmental conditions in this study.

Heritability estimates were estimated to be 0.166 (standard error = 0.071) and 0.421 (standard error = 0.211) at wind velocities of 0.3 and 0.8 $\mathrm{m \cdot s^{-1}}$ respectively. Standard errors indicate that the h^2-estimates do not differ between the two wind velocities.

The interaction between sire and wind velocity is nearly significant, suggesting the absence of cross-environmental genetic correlation (Table 2). This is supported by the r_A estimate of 0.46 and the non-significant correlation of family means across both wind conditions ($r_{32} = 0.068$; $P = 0.706$; Fig. 3).

Table 2. Results of the mixed-model analysis of variance for ballooning on the 0/1 scale as a function of sire, dam, and sire × wind

Fixed effect	Numerator d.f.	MS	*F*-value	*P*
Wind	1	1.266	11.57	0.004
Dam(Sire)	16	0.110	1.00	0.500
Sire	15	0.574	5.25	0.001
Sire × Wind	15	0.166	1.51	0.210
Error	16	0.109		

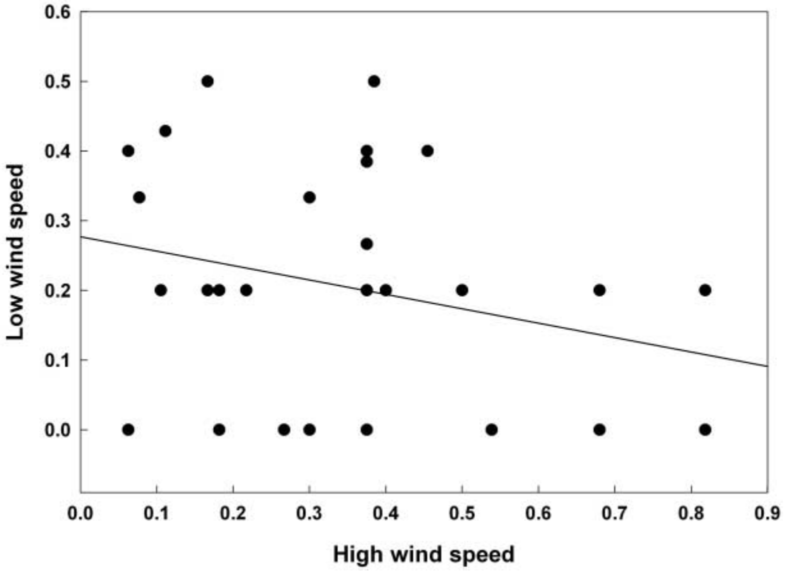

Fig. 3. Correlation between average ballooning propensity of siblings under high (0.8 $\mathrm{m \cdot s^{-1}}$) and low (0.3 $\mathrm{m \cdot s^{-1}}$) wind speeds.

DISCUSSION

We showed that dispersal motivation in the saltmarsh wolf spider *Pardosa purbeckensis*, as assessed by individual ballooning probabilities, contains a substantial additive genetic component, as reflected by the significant wind × sire population interaction, significant sire effects under both wind velocity treatments, and narrow-sense heritabilities of the liability. Similarity among siblings due to common environment effects was minimized by rearing spiders in individual containers. These estimates were not significantly different under the two wind velocities, but do suggest an increased canalization and heritability under the highest wind velocity (the 'unfavourable' environment). Moreover, we found no evidence of genetic correlations between the two environments, indicating the prevalence of independent selection on dispersal motivation at different wind velocities.

The estimated heritabilities of ballooning motivation are in line with expectations based on its behavioural category and integration level in wild populations (Stirling *et al.*, 2002). According to the latter, heritabilities of behavioural traits related to movement and foraging average 0.30, and do not differ between behaviours with different relationships to fitness. The onset of ballooning can be considered as an intermediate integrated one that comprises behaviours related to (i) detecting wind velocity, (ii) the onset of tiptoe behaviour, and (iii) the production of silk threads for effective dispersal (Bell *et al.*, 2005). Moreover, ballooning is a behaviour related to individual decision-making prior to the dispersal event and tightly linked to fitness because of direct mortality risks related to the potential (uncontrollable) dispersal distance when suitable habitat is small or when suitable habitat is highly spatially structured beyond the individual's dispersal ability (Bonte *et al.*, 2003, 2006). In contrast to movement behaviours with greater potential for dispersal-control such as cursorial dispersal (Bonte *et al.*, 2004, in press; Schooley and Wiens, 2004) and active flight by larger winged arthropods (van Dyck and Baguette, 2005), close links to fitness (i.e. survival vs. direct mortality) can be expected, with in general less heritability (e.g. Falconer, 1989; Mousseau and Roff, 1987; Merilä and Sheldon, 2000; Blanckenhorn and Heyland, 2004; Uhl *et al.*, 2004). The few available data on heritability estimates of dispersal behaviour in arthropods do substantiate this expectation: Kent and Rankin (2001) estimated the heritability of the migratory tendency in a grasshopper to be 0.5–0.6, and Li and Margolies (1994) reported heritability for ballooning propensity in mites (0.28) in line with our results.

Since mortality risks are directly related to increased wind velocity in isolated and small habitat fragments, a stronger canalization towards lower dispersal probabilities was expected under 'unfavourable' high wind velocities. Consequently, similarity in behaviour was expected to increase, eventually resulting in increased heritability estimates. Crossing reaction norms for ballooning propensity and different heritability estimates (although not statistically significant due to large standard errors) at the two wind velocities seem to substantiate this expectation. Moreover, the lack of any genetic correlation ($r_A < 0.5$) between the low- and high-wind environments suggests that selection can act independently on ballooning motivation in both wind environments. Consequently, not only do the trait means appear to be under genetic control, also their shifts in magnitude and, hence, their level of plasticity under different wind velocities (Bonte *et al.*, 2007). Our expectation of altered heritability estimates was based on evidence of stress-dependent changes in the expression of genetic variability (Hoffmann and Merilä, 1999). In general, studies addressing the effects of stress make use of traits that experience stress during development, which additionally often covary with individual morphological and physiological properties (e.g. Pakkasmaa *et al.*, 2003;

Blackenhorn and Heyland, 2004; Uhl *et al.*, 2004; Relyea, 2005). Unfavourable conditions imposed during our experiment were restricted in time and are assumed only to interfere with individual decision-making within these narrow time periods. The lower dispersal motivation at the population level at the higher wind velocity agrees with findings from a more elaborate study with genotypes from seven populations, ranging from very small to very large saltmarshes (Bonte *et al.*, 2007). Our induced wind velocities also result in dispersal trajectories >300 m, hence with net emigration into hostile habitat. This certainly provides evidence that the implemented magnitude of stress (wind velocity) is likely to impose direct fitness effects, especially in genotypes from small areas.

In conclusion, different (but not statistically so) heritability estimates of ballooning motivation and the lack of genetic correlation among the two wind environments indicate the prevalence of genetic variation in behavioural plasticity towards different wind environments in *P. purbeckensis*. Genetic variation in plasticity can be maintained on small spatial scales of only a few metres (Stratton, 1994; van Kleunen and Fisher, 2001). Given the strong temporal aspects of variation in meteorological conditions, which are additionally affected by phenological variation in hatching and juvenile development (the dispersal window), temporal variation in weather conditions, including wind velocity, is here suggested to maintain dispersal plasticity and genetic variation under different meteorological conditions. Consequently, maladaptive genotypes in small saltmarshes (i.e. genotypes promoting dispersal under high wind velocities) may only be counter-selected during periods of high wind velocities, but not so during periods of low wind velocities.

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