

Environmental and genetic background of tiptoe-initiating behaviour in the dwarfspider *Erigone atra*

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Ballooning is a widespread behavioural trait in invertebrates, which enhances passive aerial dispersal. We investigated the influence of common lineage (family effect) and postnatal environmental conditions on latency to initiate preballooning tiptoe behaviour (ballooning latency) in the dwarfspider *Erigone atra* (Blackwall, 1841). The ballooning latency of individual spiders was tested in a specially designed test chamber. In a 3-week experiment, in which the spiders were fed only during the first day of each week, ballooning latency had low repeatability at weekly intervals. Ballooning latency declined with increasing food deprivation during the first week but not during the second and the third weeks. At intervals of less than 1 h, however, ballooning latency showed high repeatability. We also investigated whether maternal and postnatal environmental conditions (i.e. during juvenile development) influence phenotypic variation in ballooning latency. We reared offspring of several families under two feeding and two temperature conditions. Environmental conditions explained more variation in ballooning latency than family. Ballooning latency was lower in spiders reared at 20°C than in those reared at 15°C. In addition, spiderlings fed four prey per 3 days were faster ballooners than those fed only four prey per week. An interaction between factors was present, indicating the existence of different reaction norms between the two environmental conditions. The expression of ballooning latency behaviour thus strongly depends on current nutrition, feeding history and the feeding and temperature conditions during juvenile development.

Aerial dispersal is common among terrestrial insects and spiders. In the latter, this mode of dispersal is known as ballooning. The spider climbs to an elevated starting point, stretches its legs and raises its abdomen (tiptoe behaviour); it then produces long silk threads and is finally carried up by the air current (Jones 1996a, b). Aerial dispersal is effective for both distant migration (possibly affecting gene flow) and local dispersal (Thomas 1996), especially in ephemeral but highly productive habitats where rapid movement under unfavourable conditions is important for survival (Legel & Van Wingerden 1980; Van Wingerden 1980; Morse 1993; Duffey 1998). Tiptoe behaviour is typical of aerial dispersal in spiders of the Linyphiidae and juvenile Lycosidae and can be easily observed under laboratory conditions (Weyman 1993). *Erigone atra*, one of the commonest spiders of open habitats in the temperate regions of the northern hemi-

sphere, has a strongly developed ballooning behaviour. This species is often one of the first pioneers on regularly disturbed, especially agricultural, land (De Keer & Maelfait 1988a, b).

Ballooning in spiders has mainly been studied in field conditions, especially within the framework of timing of dispersal (Dean & Sterling 1985; Greenstone et al. 1987; Blandenier & Fürst 1998; Bonte et al. 1998) and in relation to spider densities and activities in the field (Greenstone et al. 1985; Weyman et al. 1995). Laboratory studies have largely focused on the relation between aeronautic behaviour and meteorological conditions such as wind velocity and temperature (Van Wingerden & Vugts 1974; Vugts & Van Wingerden 1976; Greenstone 1990), and on the importance of crowding and food shortage as a trigger for this behaviour (Legel & Van Wingerden 1980). Ballooning is triggered by acute food shortage (Weyman et al. 1994), low wind velocities (<3 m/s) and a high temperature inversion during the morning (Richter 1970; Van Wingerden & Vugts 1974; Vugts & Van Wingerden 1976; Greenstone 1990; Duffey 1998), and its frequency differs between species (Richter

1970; Van Wingerden 1980; Greenstone 1982; Miller 1984). Differences between populations, however, have not been unambiguously demonstrated (Richter 1971).

Little experimental work has been carried out on factors underlying the initiation of ballooning behaviour, or on genetic variance underlying phenotypic variation (Weyman 1993). Several studies have shown that wing dimorphism in insects is under polygenic control (Järvinen & Vepsäläinen 1976; Roff 1986; Kaitala 1988; Desender 1989) and Li & Margolies (1993) found additive genetic variation for dispersal behaviour in the two-spotted spider mite, *Tetranychus urticae*. In the latter study, however, nonadditive genetic variation and maternal effects or common environmental variation explained the largest part of the phenotypic variation, and no covariation with fecundity and sex ratio was found. A major problem exists in estimating heritability of behavioural traits because of their low level of repeatability, caused by difficulties in keeping experimental conditions or the individual's internal state constant (Kecic & Marinkov 1974).

We investigated (1) the repeatability of preballooning behaviour, (2) the extent to which variation is determined by environmental circumstances during juvenile development, and (3) the extent to which a family effect is present. Such factors may contribute to similarity in offspring dispersal behaviour, as demonstrated by Massot & Clobert (2000). Family effects include maternal effects and possible additive heritabilities. Postnatal effects include common environmental conditions and (social) interactions between siblings. Relations between offspring dispersal and maternal and offspring characteristics can result from both genetic and environmental factors (Kirkpatrick & Lande 1989) and are very informative about the nature of dispersal. Our aim was therefore to investigate whether family effects or postnatal environmental conditions influence preballooning behaviour (i.e. the latency to show tiptoe behaviour).

Although behaviours such as climbing vegetation and taking off are also important factors in aerial dispersal (Weyman 1993), studies on the latency to initiate tiptoe behaviour are needed to understand variation in the spider's motivation to disperse by ballooning under suitable meteorological conditions. Fast-reacting individuals under laboratory conditions are more likely to balloon under variable weather (wind velocity) conditions and under sudden unsuitable environmental conditions in which spiders have to escape from their original habitat.

METHODS

General Methods

We tested the propensity to express tiptoe behaviour under constant climatological conditions, using a test chamber based on the recommendations of Legel & Van Wingerden (1980). Spiders were placed on a plastic frame in an air tunnel with upward currents at a temperature of $30 \pm 2^\circ\text{C}$, aerial humidity of 40–50% and a light breeze, velocity 1–1.2 m/s. To prevent the spiders from escaping,

we placed the frame in a bath of water. Because all individuals expressed the tiptoe behaviour within 10 min, we measured the latency (to the nearest second) of the spider to initiate this behaviour (ballooning latency) from the onset of wind turbulence. To be valid, a minimum of 3 s of constant tiptoe behaviour needed to be observed. With the exception of the 3-week repeatability experiment (see below), all individuals were tested 1 day after moulting to the adult stage, to minimize variation in internal state. Spiders were not acclimatized to the climate conditions in the test chamber.

We collected gravid female spiders randomly at the end of September 1999 in grass tussocks in a pasture of the Westhoek dune reserve in De Panne, Belgium. Because the species is abundant throughout the year, we did not select individuals that were dependent on ballooning to colonize sites. We used the adult instars of the females' offspring for laboratory experiments. Spiderlings were reared in petri dishes (diameter 5 cm) on plaster of Paris under a relative humidity close to saturation and a light:dark cycle of 16:8 h. The collembolan *Isotoma viridis* was used as prey. Because we wanted to investigate how different environmental conditions influence ballooning behaviour, we imposed four different rearing treatments by combining two temperature regimes (low: 15°C ; high: 20°C) and two diet regimes (well fed: four prey/3 days; poorly fed: four prey/week). All prey offered were consumed, and mortality was low (5.2%).

Latency data were ln transformed and did not differ from a normal distribution (Kolmogorov–Smirnov test: NS).

Repeatability and Acute Stress

To measure repeatability over short intervals, we tested 38 randomly selected individuals twice within 1 h. Individual ballooning latencies were compared by intraclass correlation coefficients (t), calculated from a one-way ANOVA with individual as factor (Lessels & Boag 1987; Boake 1989; Sokal & Rohlf 1995). An intraclass correlation coefficient close to 1 indicates a high repeatability, one close to zero none. We examined the repeatability at longer intervals, that is, with variable periods of food stress, in 20 spiders kept at 20°C during a 3-week experiment, in which they were fed only on the first day of each week. Consequently, they experienced increasing food deprivation effects for the rest of the week. Ballooning latency was tested each day. Intraclass correlation coefficients for ballooning latency were calculated between days when spiders were assumed to be in the same nutritional state (day after spiders were fed, 1-week intervals). All analyses were performed with SAS 8.1 and statistica (Statsoft 2000); variation caused by the random individual effect (intraclass correlation) was tested against a model including all variance components (chi-square test of difference in log likelihood). Statistical tests were two tailed.

Developmental Conditions and Family

We randomly assigned spiderlings from 13 females to the four rearing conditions described above, and tested

them 1 day after final moult under well-fed conditions. Preliminary experiments indicated that gender did not influence ballooning latency (unpublished data). We applied a General Linear Model with type III sum of squares, family (genotype) as a random factor and temperature and feeding conditions as fixed factors. In this way, our data were analysed in a quantitative genetic framework with genotypexenvironment interaction, whereby genotype included nonadditive components, prenatal maternal and paternal effects. We used 284 individual spiders from 13 families (mean 5.04 siblings/treatment). Variance estimates, contributed by special environmental effects (as a consequence of random developmental noise and microenvironmental variation), genotype and genotypexenvironment interactions were calculated from the expected mean squares under a mixed model (Lynch & Walsh 1998). Because of the specific mean squares configuration, fixed (macro-environmental) factors did not explain any of the variation (Lynch & Walsh 1998).

Relations with Life History Traits

We measured development time to maturity (to the nearest day) and size of the spider (cephalothorax size in mm² digitized under a 50x binocular microscope) for the offspring of 24 females reared with prey ad libitum at 20°C. These data were used for the analysis of possible correlations with the ballooning latency. In addition, we measured female size (measured in the same way as for the offspring) and the number of offspring in the first cocoon (fecundity as maternal fitness characteristic). The sex ratio in the first cocoon was also determined. Because fecundity was correlated with the size of the female (Pearson correlation: $r_{148}=0.268$, $P<0.05$), we used residuals of the regression of number of eggs in the first cocoon on female size as a fitness measure.

RESULTS

Repeatability and Acute Stress

Ballooning latency did not differ significantly between the two tests conducted within 1 h and was highly repeatable ($\bar{X}\pm\text{SD}$; test 1: 110.66 ± 66.90 s; test 2: 87.94 ± 50.91 s; intraclass correlation $t=0.781$; random effect: $\chi^2_1=43.5$, $P<0.001$). At 1-week intervals it decreased and was less repeatable (range 0.306–0.708). Ballooning latency decreased significantly over the first week of the 3-week experiment (Pearson correlation: $r_{18}=0.270$, $P<0.05$) but not during the second ($r_{18}=0.014$, NS) and the third weeks ($r_{18}=0.0008$, NS; Fig. 1).

Developmental Conditions and Family

Phenotypic variation in ballooning latency could be attributed to feeding and temperature conditions during juvenile development, but not to genotypic (family) effects (Table 1). Levels of ballooning latency were significantly higher at 15°C than at 20°C and higher with the

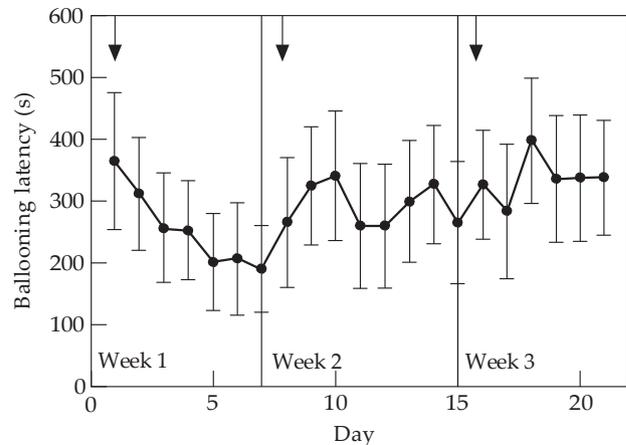


Figure 1. Ballooning latency ($\bar{X}\pm 95\%$ confidence intervals, s) over a 3-week experiment in which 20 spiders were fed only on the first day of the week (arrow).

poor diet (Fig. 2). Latency differed significantly between temperatures ($\bar{X}\pm\text{SE}$; 15°C: 4.979 ± 0.783 s; 20°C: 5.493 ± 0.541 s; post hoc Scheffé test: $P<0.001$) but not between diet treatments (poorly fed: 5.251 ± 0.625 s; well fed: 5.320 ± 0.674 s; post hoc Scheffé test: NS). The interaction between temperature and diet was, however, significant: when poorly fed, spiderlings reared at 20°C increased ballooning latencies, and those reared at 15°C decreased it.

Genetic variation explained 29.2% of the total phenotypic variation (partitioned as 16.0% for genotype and 13.2% for all genotypexenvironment interactions); the remaining variation could be attributed to micro-environmental variation (70.8%; Table 1).

Relations with Life History Traits

For males and females separately, no relation between ballooning latency and size at maturity was found (males were significantly larger than females: t test: $t_{236}=10.45$, $P<0.001$; Table 2). Development time to maturity was independent of sex ($t_{278}=0.116$, NS) and did not show a significant correlation with ballooning latency for the well-fed individuals reared at 20°C (Table 2). If we include all observations from the four-environments experiment, a significant positive correlation was found with development time increasing in the order high temperature/well fed, high temperature/poorly fed, low temperature/well fed and low temperature/poorly fed. Both temperature and diet contributed to this difference (ANOVA: temperature effect: $F_{1,280}=354.921$, $P<0.001$; diet effect: $F_{1,280}=33.927$, $P<0.001$). No significant relations with maternal life history traits were found (Table 2).

DISCUSSION

Our laboratory experiments showed high repeatability of latency to express preballooning behaviour under stress (when the spider had to escape from the test chamber to survive at a relatively high temperature) at short intervals

Table 1. Results of the GLM for ballooning latency (ln transformed) on the factors temperature, diet (both fixed) and family (random)

Factor	Sum of squares	df	Mean square	F	P	Variance estimates
Temperature	8.456	1	8.456	8.222	0.012	NE
Diet	1.927	1	1.927	5.159	0.036	NE
Family	30.948	12	2.579	3.720	0.159	0.105
Temperature×Diet	3.201	1	3.201	4.327	0.032	NE
Temperature×Family	13.413	12	1.117	1.426	0.273	0.065
Diet×Family	4.308	12	0.359	0.458	0.904	-0.010
Temperature×Diet×Family	9.402	12	0.784	1.648	0.070	0.032
Error	121.424	261	0.465			0.465

NE: No estimates available.

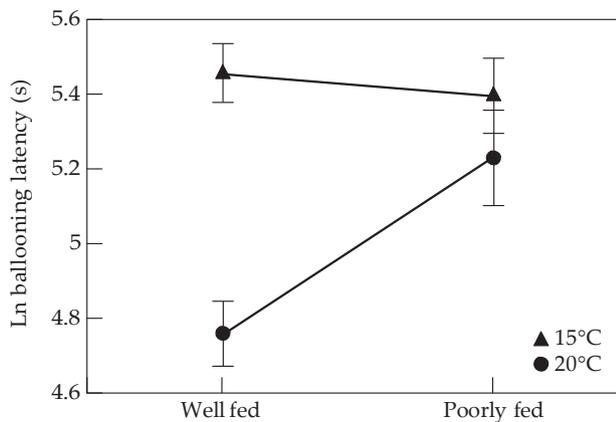


Figure 2. Ballooning latency ($\bar{X} \pm SE$, s) of spiders that, as juveniles, were reared at 15 or 20°C and were either well fed or poorly fed (four prey per 3 or 7 days).

of 1 h, but low repeatability at longer intervals of a week. Phenotypic variation was determined mainly by environmental conditions and less so by genotypic effects. Relations with individual and maternal fitness characteristics were not found.

Our results confirm that tiptoe behaviour in erigonid spiders is strongly influenced by food deprivation (Van Wingerden & Vughts 1974; Legel & Van Wingerden 1980; Weyman & Jepson 1994; Weyman et al. 1994). This pattern was found only during the first week of food deprivation, however, and not during food deprivation in the next 2 weeks. This result indicates that ballooning latency depends not only on acute feeding stress but also on feeding history and age. Because of this low repeatability, it is difficult to make representative multiple measurements and to estimate the trait heritability under different environmental and internal conditions. The lack of multiple measurements has led to underestimation of the levels of heritability of courtship and mating speed in *Drosophila* (Hoffmann 1999). The male-biased sex ratio during ballooning in the field (Blandenier & Fürst 1998; Bonte et al. 1998) cannot be attributed to a different tiptoe-initiating behaviour, because the latter was independent of sex.

Different environmental conditions during juvenile development markedly affected the latency to initiate

preballooning behaviour. Both the feeding regime and the temperature had a significant effect. The effect of temperature was clear: spiders reared at 20°C took off faster than those reared at 15°C. The finding that the juvenile diet influenced the adult's ballooning latency was as predicted; however, our results showed an effect of temperature as well. Ballooning latency was shorter for spiders that were well fed during development when the temperature was high (20°C), but at the lower breeding temperature, there was only a marginally significant difference between diets. An interaction between diet and temperature was thus present, indicating a complex reaction of spiders to different postnatal environmental factors.

The strong effect of temperature during rearing on ballooning latency may be an inherent physiological response. Flight activity in *Oncopeltus* also changes significantly with temperature during development (Dingle 1968), suggesting a physiological depression near temperatures at the threshold where reproduction is possible. In the carabid beetle *Pogonus chalceus*, where dispersal potential is related to wing size, temperature during development did not alter the relative wing length (Desender 1989). High temperatures over the summer could thus act as an extra trigger for the stimulation of the mass late-summer ballooning commonly observed in *E. atra* (Bonte et al. 1998; Duffey 1998), although an interaction with temperature during ballooning is to be expected. Nevertheless, our data indicate that ballooning latency is influenced by physiological responses to environmental circumstances during juvenile development. Mothers are thus able to influence the ballooning initiation of their offspring by the choice of habitat for reproduction.

Different nutritional conditions during juvenile development induced different behavioural ballooning patterns, in contrast to acute food stress, which is the final trigger for ballooning in many spiders (Van Wingerden & Vughts 1974; Legel & Van Wingerden 1980; Weyman & Jepson 1994; Weyman et al. 1994; Bonte & Maelfait 2001). Our findings contradict those of Legel & Van Wingerden (1980), who found a lower percentage of ballooners in tested spiders when individuals were reared under well-fed and medium-starved regimes (40 and 37.5%) than with greater levels of starvation. Their model

Table 2. Life history traits of offspring and their mother, and correlations between traits and ballooning latency

Life history trait	Mean value±SD	N	Correlation	
			r*	P
Offspring				
Development time (days)				
All conditions	39.23±5.18	280	0.220	<0.001
At 20°C, spiders well fed	22.05±3.34	248	0.067	NS
Cephalothorax size at maturity (mm ²)				
Males	3.34±0.21	117	0.142	NS
Females	3.09±0.16	125	0.042	NS
Mother				
Offspring sex ratio (males/females)	0.87±0.38	24	-0.129	NS
Adult cephalothorax size (mm ²)	3.20±0.03	24	-0.259	NS
Number of offspring in first cocoon	14.00±3.95	24	0.146	NS
Residuals of offspring on mother's size	—	24	-0.306	NS

*Pearson correlations for offspring traits and Spearman rank correlations for mother's traits.

organism was *Erigone arctica* (White, 1852), a sister species typical of salt marshes. Although the power of their experiment was too low for appropriate statistics, their results indicate again that feeding conditions during development alter ballooning capacity. Different species can apparently react in different ways to changing environmental conditions. Since the temperature during rearing in their experiment was rather high (room temperature between 18 and 23°C), similar results to ours could be expected.

Our results suggest that ballooning latencies in *E. atra* are short only in highly productive habitats, where prey are abundant and temperatures high. As we observed covariance between development time in the four treatments and ballooning latency, the variation we observed in ballooning latency can be explained by variation in development time. In our experiment, however, ballooning latency was not correlated with development time within the separate rearing conditions and so development time is probably not the main trigger responsible for the observed variation in ballooning latency under laboratory conditions.

Family effects explained about 16% of the observed phenotypic variation. Although not statistically significant (only 13 families were included in the quantitative study), this genotypic source of variation was not negligible. It stresses the importance and interaction of genetic components in the expression of behavioural traits, narrowly linked to dispersal. This biologically relevant, low genotypic source of variation is concordant with Roff & Mousseau's (1987) and Hoffmann's (1999) findings of overall low heritabilities for behavioural traits. We did not find any relation between offspring ballooning latency and maternal fitness characteristics. The probability of ballooning by young crab spiders, *Misumena vatia*, also did not differ with clutch size or individual size (Morse 1993). Morse (1993) also found an effect of substrate, which was related to immediate prey availability. Consequently, the choice of nest sites (substrate) by the spiderlings' mothers indirectly affected the spiderlings'

dispersal behaviour. Our results are thus in agreement with Morse's (1993) findings that intraspecific variation in spider ballooning is only marginally determined by evolutionary components. More empirical research is needed to understand the possible sources of variation in ballooning behaviour.

In insects with distinct dispersal characteristics such as wing polymorphisms and differentiated muscle development, maternal and additive genetic effects influence the total phenotypic variation (e.g. Janssen et al. 1988; Leamy 1988; Desender 1989). In full and half sibling, direct and indirect selection experiments, Li & Margolies (1993, 1994) found a relatively high heritability of ballooning latency in the arachnid (phytophagic) mite *Tetranychus urticae*. Li & Margolies minimized the residual variance during the experiments to 43–60%; and they estimated the additive genetic component to be 22.39%. Because of the strong influence of environmental factors and the impossibility of conducting multiple measurements, analogous experiments on ballooning behaviour in spiders are probably difficult to conduct in a standardized way.

In summary, we conclude that, in addition to (extensively documented) acute starvation, environmental variation during juvenile development influences ballooning latency in *E. atra* under our laboratory conditions. The habitat choice of the mother is therefore likely to influence offspring ballooning behaviour. A low, but biologically relevant, genotypic source of variation was, however, detected indicating that environment and genotype sum and interact in the expression of this dispersal-linked behavioural trait.

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