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Repeatability of dispersal behaviour in a common dwarf spider: evidence for different mechanisms behind short and long distance dispersal

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ABSTRACT

1. The response of dispersal towards evolution largely depends on its heritability for which upper limits are determined by the trait's repeatability.

2. In the Linyphiid spider *E. atra*, we are able to separate long- and short distance dispersal behaviours (respectively ballooning and rappelling) under laboratory conditions. By performing repeated behavioural trials for females, we show that average dispersal trait values decrease with increasing testing days. By comparing mated and unmated individuals during two periods (before and after mating for the mated group and the same two periods for the unmated group), we show that mating has no effect on the mean displayed dispersal behaviour or its within-individual variation. Repeatabilities were high and consistent for ballooning motivation but not for rappelling.

3. Ballooning motivation can be regarded as highly individual-specific behaviour, while general pre-dispersal and rappelling behaviours showed more individual variation. Such difference in repeatability between long- and short distance dispersal suggests that short- and long-distance dispersal events are triggered by different ecological and evolutionary mechanisms.

INTRODUCTION

Dispersal refers to the movement of individuals or propagules with potential consequences for gene flow across space (Kokko & Lopez-Sepulcre, 2006; Ronce, 2007) and comprises three consecutive stages: emigration, transfer and immigration (Ims & Yoccoz, 1997; Bowler & Benton, 2005). It allows escape from areas with unfavourable conditions and influences the genetic cohesion of species across space and their global persistence despite local extinctions (Bowler & Benton, 2005; Ronce, 2007). Dispersal has been shown to affect speciation, inbreeding depression, and the evolution of sociality and many life history traits (Clobert *et al.*, 2001; Ronce, 2007). Because dispersal strongly affects the dynamics and evolution of spatially structured populations (Ronce, 2007), it is also considered a key life history trait driving population responses to changing environments. Understanding its causes and consequences is therefore a prerequisite when aiming to manage natural populations within the context of conservation (Kokko & Lopez-Sepulcre, 2006) and ecosystem functioning (Kremen, 2007).

While dispersal is often considered as a fixed trait, especially in modelling (Clobert *et al.*,2001; Ronce, 2007), there is growing evidence that dispersal functions are largely condition-dependent (Bowler & Benton, 2005). This implies that dispersal should be regarded as a plastic trait with very specific responses towards internal and external conditions (Ronce, 2007). Consequently, dispersing individuals should not be considered as a random-subset of their source populations. Mating status is one of the factors that may greatly influence dispersal decisions. Limited time windows for mating and subsequent decreasing expectations of successful reproduction should motivate unmated females to disperse as time is progressing. These patterns were shown, for example in spider mites (Li & Margolies, 1993; Suiter & Gould, 1992).

Dispersal studies often focus on movement behaviours and it is not always clear whether observed patterns or underlying mechanisms are really dispersal specific (Van Dyck

& Baguette, 2005). For instance, butterflies fly often large distances for foraging or mate location and have subsequently large home-ranges (Van Dyck & Baguette, 2005). Birds may make exploratory forays outside their home range preparatory to dispersal (Dingemanse et al. 2003). These behaviours are therefore not related to dispersal as such. Interpreting these movements as dispersal movements is consequently dangerous and can lead to idiosynchratic insights. Similarly in spiders, short distance movements at the ground level are often the result of random local movements that eventually lead to the colonization of non-natal habitat (Bonte *et al.*, 2003b; 2004). In the same vein, smaller spiders use silk as transport medium to 'travel' through the air; Bell *et al.*, 2005). Smaller spiders belonging to the Linyphiidae, disperse predominantly by using silk threads as either a sail (so-called *ballooning*) for long-distance dispersal or a bridging thread (so-called *rappelling*) for short-distance dispersal. Both dispersal modes are preceded by tiptoe-behaviour, which involves stereotyped actions such as stretching of the legs, rising of the abdomen and production of long silk threads (Bell *et al.*, 2005). Prior to ballooning, spiders produce silk threads and then take-off attached to the thread for distances of up to several hundred meters (Thomas *et al.*, 2003). In case of rappelling, the distal ends of the silk threads become attached to a substrate, and are used to bridge short distances. Because these behavioural components can be quantified under standardized laboratory conditions, spiders can be regarded as excellent biological models to test dispersal theory in a natural system. In earlier contributions, we made use of these properties to document evolution of dispersal propensity both between (Bonte *et al.*, 2003a) and within species (Bonte *et al.* 2006, 2007). Because we focused predominantly on wolf spiders that perform tiptoe behaviour only for ballooning, we were able to show that long-distance dispersal is determined by heritable variation (Bonte & Lens, 2007), but that its expression also depends on the prevailing environmental conditions, like wind velocity (Bonte *et al.*, 2007). Because some Linyphiid spiders perform both short- and long distance behaviour under laboratory conditions and in natural situations, they comprise excellent model organisms to contrast evolutionary mechanisms of both dispersal

modes (Bonte et al. 2008b). These dispersals are performed in the adult life phase, but females show generally higher dispersal motivation than males (Bonte et al. 2008b).

Experimental studies of tiptoe behaviour in Linyphidae as a proxy for dispersal go back to earlier work from Legel & Van Wingerden (1980), Weyman & Jepson (1994) Weyman et al. (1994, 1995). Different attempts to estimate the trait heritability resulted in often completely different estimates ranging from 0 to 0.30 (Bonte *et a*l., 2003; unpub. data). One possible reason for these variable results is that the studied behaviour does not necessarily precede the same movement behaviour. Indeed, as outlined above, tiptoe behaviour can both precede long and short-distance dispersal (or movement). Ronce (2007) argues correctly that short- and long-distance dispersal events may rely on different mechanisms from a mechanical and evolutionary point-of-view or are even accomplished by different types of individuals.

Because only traits that are manifested consistently within individuals as well as differing between individuals can respond to selection (Boake, 1989), we studied repeatability of long- and short distance dispersal in a spider to infer upper limits of heritability. We additionally assessed the consistency of dispersal traits and its between-individual variation in relation to mating status because changes in internal state may heavily influence dispersal decision making (Bonte et al. 2008b).

MATERIAL AND METHODS

Behavioural trials - Experiments were conducted with 36 female offspring from field caught mated females *Erigone atra* (collected in crops in the vicinity of Ghent, September 2007). These females were individually bred under standardized conditions (temperature of 25°C, RH approx 70% and prey, i.e. collembolans and fruit flies *ad libitum*). Seven days after final moulting we started the behavioural trials. All females were individually, daily screened for their aeronautic behaviour in a wind tunnel (cfr. Bonte et al. 2008a,b) with upward wind velocity of 1.2 ± 0.2 m/s and ambient temperature of 25°C. All females were acclimatized for one hour to the conditions of the wind tunnel. During trials of 15', we recorded tiptoe frequency, duration of the tiptoe behaviour as general pre-dispersal behaviours. Depending on the performed dispersal behaviour and the frequency, probability and duration of each rappelling and ballooning could be derived. The 'frequency' comprises the number of times an individual ballooned or rappelled during a trial; the 'probability' reflects whether an individual showed ballooning or rappelling at least once during a trial. As argued by Bonte et al. (2008b), the frequency and probability of the behaviours are regarded as a measure for dispersal motivation; the duration of tiptoe behaviour prior to a dispersal event reflects the investment in silk thread length, which related to the potential dispersal distance for ballooning (Bonte *et al.*, 2008a) or the effective distance moved during rappelling.

During the behavioural trials, spiders were allowed to show multiple dispersal events to quantify dispersal motivation. Therefore, individuals were gently put back after dispersal on the platform (hence minimizing manipulation by the experimenter) after removing the previously produced silk threads with a small brush. In case individuals performed multiple ballooning or rappelling events, we calculated the average value during each trial. During the first five days, all females were tested in unmated condition. On day six, half of the females (randomly assigned) were mated with similarly bred males. During this day and the following day, no experiments were conducted. On day eight, all females were again tested for their aeronautic behaviour during four subsequent days.

1   ***Data analysis -*** Repeatability is directly useful as a measure of the within-individual

2   consistency of behaviour. Repeatability and consistency are related but not synonymous

3   terms describing behaviour (Cummings & Mollaghan, 2006). Repeatability is defined by the

4   intraclass correlation (*r),* which indicates the proportion of total variation in a trait that is due

5   to differences between individuals (Falconer & Mackay, 1996). It is based on repeated

6   measures of the same individuals followed by an analysis of variance. Since it is computed

7   as a ratio, its values are always expressed relative to the variation between individuals. A low

8   repeatability may therefore indicate either low overall variation in behaviour (low variation

9   between and within females) or high variation due to random patterns. Its usual application

10   has been to set an upper limit on heritability but it may also be useful for studies of

11   stereotypy of behaviour (Boake, 1989). Consistency, on the other hand, is a term we use to

12   evaluate variation of behaviour relative to each individual's successive performances. This

13   measure evaluates an individual's consistency independent of variation across individuals.

14   We used repeated measure mixed models to analyze the daily performed (test day is

15   the repeated unit) behaviours as a function of the period (period up to mating *versus* the

16   period after mating in half of the individuals) and the induced mating treatment. An interaction

17   between factors *mating* and *period* should indicate that females show different behaviours in

18   the period prior to and after the induction of mating, depending on their mating status (mated

19   versus unmated). We modelled the individual*period variance component in order to assess

20   how mating status affected the between-individual variation in behaviour. When this

21   interaction component (random effect) approached zero, we included only the factor

22   'individual' as a repeated measure (repeated tests on subsequent days; random factor) to

23   test overall repeatability.

24   Depending on the error function, we used mixed models with a Binomial distribution

25   (logit-link function) for ballooning- or rappelling incidence, a Poisson distribution for

26   frequencies of performed behaviours (log-link function) and a normal distribution for duration

27   of tiptoe displays. An additional regression was performed with 'test day' as a continuous

28   factor (instead of period as a fixed one) in order to test whether the behaviours decreased or

1   increased systematically with time. We used the Satterthwaite procedure to approximate

2   denominator degrees of freedom. Analyses were conducted with Proc Mixed (normal

3   models) and Proc Glimmix (Poisson and Binomial models). Covariance tests (Z-tests) were

4   used to test the significance of the variance components related to repeated individual tests.

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6   Repeatability was calculated as the intraclass correlation coefficient (*r*), i.e. the ratio of

7   between-individual variance (s^2_A) to the total variance (V_t = between + within: $s^2_A + s^2_R$). An

8   intraclass correlation coefficient close to 1 indicates a high repeatability, one close to zero

9   none. Monte Carlo permutations (10000 permutations) were used to derive the standard

10   error on the derived intraclass correlation coefficients.

11   Consistency of behaviours that refer to a frequency or duration of each female were

12   calculated as coefficient of variation or the standard deviation expressed as a fraction of the

13   mean (*CV*=σ/mean; Cummings & Mollaghan, 2006). For the duration of tiptoe behaviour

14   preceding rappelling and ballooning, *CV* is calculated for the trials in which an individual

15   effectively performed the respective dispersal behaviour. For each individual's probability to

16   perform either ballooning or rappelling during a behavioural trial, we calculated the frequency

17   of the performed behaviour during all repeated trials. High values for the latter subsequently

18   indicates consistent performance of either rappelling or ballooning over all behavioural trials.

19   For ease of interpretation, we took the inverse of *CV*, so large high values also indicate high

20   consistency for these behaviours. Average values and standard errors over all tested

21   females (n=37) are given.

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RESULTS

Mating status had no effect on the between-individual variation in any of the behavioural traits ($\sigma_{individual*mating} \sim 0$ for all behaviours). Therefore we have calculated trait repeatability over all test days, irrespective of the individual's mating status. The repeatability of the behaviours showed considerable variation (Fig. 1). Repeatability for general pre-dispersal behaviours (tiptoe frequency and tiptoe duration) and the behaviours related to short distance dispersal (rappelling) showed overall low repeatabilities. The repeatability of rappelling frequency was low (0.13±0.05) but significantly different from zero. All behaviours related to long distance dispersal were significantly larger than zero and were highest for ballooning probability and ballooning frequency (r > 0.40).

The consistency of tiptoe frequency, ballooning and rappelling duration were considerably higher than those for ballooning and rappelling frequency (Table 1). Consistency of ballooning and rappelling probability was high and deviated significantly from random (i.e., frequency of 0.5) for both (95% confidence intervals rappelling: [0.62-0.74], 95% confidence intervals ballooning: [0.75-0.85]).

The period in which the tests were performed had the most prominent effect on the expressed dispersal behaviour (Table 2). The duration of the tiptoe behaviour prior to effective rappelling and ballooning events did not differ between the two periods. The average tiptoe duration was on average 1.66±0.68SE seconds shorter in the second period. The frequency of the performed tiptoe (-1.34±0.28SE events), ballooning (-0.19±0.07SE) and rappelling (-0.50±0.14SE) behaviour was lower in the second period compared to the first one. Similarly, the probability that an individual performed ballooning or rappelling decreased respectively 0.10±0.06SE and 0.21±0.06SE. For ballooning probability, however, the difference tended to be more pronounced for unmated females in the second period (-17±0.05 SE for unmated females compared to -0.38±0.07SE for females that are mated in

1   between both testing periods). The values of the behaviours decreased gradually, as can be

2   seen in the regression analyses (Table 2).

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DISCUSSION

Female *Erigone atra* show a significant decrease in dispersal behaviour during daily repeated behavioural trials. No effects of mating status were found, despite a trend of decreasing ballooning activity in unmated, but not in mated females. Repeatabilities of general pre-dispersal behaviours, rappelling behaviour and the duration of the tiptoe behaviour prior to ballooning were low. In contrast, repeatabilities of ballooning probability and frequency were high. High individual consistency of tiptoe frequency, duration of the tiptoe behaviour prior to rappelling and ballooning probability indicate that overall low repeatabilities are due to both low within- and between individual variation. In contrast, high repeatability and consistency of ballooning probability show the presence of strong between-individual and low within-individual variation. Consequently, ballooning motivation should be regarded as highly individual-specific behaviour, while general pre-dispersal and rappelling behaviours showed more within-individual variation.

Our study demonstrates that the quantification of tiptoe behaviour in *Erigone* (and probably all Linyphiid spiders) without considering the subsequent dispersal mode will largely hide evolutionary and ecological patterns that underlie the dispersal behaviour. The phenotypic variation in dispersal behaviour provides the basis for natural selection. Since repeatability is a measure that compares the relative variation between and within individuals, it may set an upper bound for heritability, although it is not its direct substitute (Boake, 1989). Our repeatability estimates indicate high within-individual variation for general pre-dispersal behaviour. Therefore, we could falsely deduce that dispersal in spiders is predominantly regulated by plasticity. Low repeatability for tiptoe behaviour at longer time frames has been previously reported by Bonte *et al.* (2003a). When considering short-distance (rappelling) and long-distance dispersal (ballooning) separately, we found that this low repeatability only holds for rappelling. In contrast, long distance dispersal (i.e., ballooning motivation) was characterised by high repeatabilities and consistency. An individual's ballooning behaviour is therefore expected to be at least partly heritable and similar under

1   altered environmental conditions. This does, however, not implicate that the behaviour is

2   fixed over all environmental conditions because the trait's expression may be partially

3   modulated by body condition. As previously shown, dispersal behaviours may vary with

4   temperature during development (Bonte *et al.*, 2003a; Bonte *et al.* 2008b) or starvation

5   during the adult life phase (Legel & Van Wingerden 1980; Weyman *et al.* 1994; Bonte *et al.*,

6   2008a). The decrease of many dispersal trait values during the subsequent repeated trials

7   suggests at least that either aging or experience affect the trait expression, but not mating

8   status as such.

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10   From a more conceptual point-of-view, our experiments point out (i) that dispersal

11   should be considered as a non-fixed trait and (ii) that long- and short distance dispersal are

12   shaped by different ecological and evolutionary mechanisms. This is the first study to report

13   differences in repeatability between long- and short distance dispersal and therefore confirms

14   the predictions that short- and long-distance dispersal events rely on different mechanisms

15   (Higgins *et al.*, 2003) and that they are potentially accomplished by different types of

16   individuals (Ronce, 2007). This implies that, at least in our model system, long-distance

17   dispersers are a non-random subsample of the population, while short distance dispersal is

18   expressed in a more random way. Of course, the apparent random patterns in short distance

19   behaviour can be the result of more subtle reaction norms towards environmental conditions

20   that change at much shorter time intervals or due to the specific testing conditions that do not

21   induce strong patterns (cfr. Bonte *et al.*, 2007). Additionally, it is not unreasonable that

22   variation in short-distance displacement is governed by mechanisms related to different

23   selection pressures than long distance dispersal (e.g., mate location, kin competition *versus*

24   escaping habitat deterioration; Ronce, 2007) or by pressures related to optimal foraging (Van

25   Dyck & Baguette, 2005). Therefore, decision making for short distance dispersal can be

26   expected to be based on information about the environment over a short time and small

27   spatial scales and should therefore favour plasticity. In contrast, decisions on long-distance

dispersal should be based on information that is gathered at longer time and larger spatial scales, i.e. inherited (both genetic and non-genetic) information on the stability of the habitat.

Although a high ballooning repeatability does not automatically imply that the trait as such shows heritable variation, it at least demonstrates that trait is largely fixed during adulthood with strong variation among individuals. Effects of common environment or maternal effects are evident in other mechanisms behind the similarity in ballooning behaviour within individuals (cfr. estimated broad sense heritability; Falconer & Mackay, 1996). The presence of additive variation for ballooning propensity in juvenile wolf spiders (Bonte & Lens, 2007) and paternal influences on the expression of ballooning behaviour (Bonte et al., 2008b) suggest that the expression can be under genetic control, although more appropriate experiments are needed to validate this. However, for ballooning motivation, we noticed a tendency of decreased expression during the repeated trials too, although mainly for unmated females. Aging or experience with the behavioural trials induces consequently systematic changes in the ballooning dispersal behaviour, thereby conserving the prevalent genetic between-individual variation.

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1 *Table 1. Consistency of the different dispersal and tiptoe behaviours (mean values and standard error for*

2 *all females, n=36). The consistency of behaviours recorded as either frequencies or duration are depicted*

3 *as 1/CV (see text); those for ballooning or rappelling probability are calculated as the frequency of*

4 *behaviours in repeated behavioural trials. Values can consequently not be compared between probability*

5 *measurements and other (frequency, duration) behaviours. Large values indicate high consistency of the*

6 *behaviour.*

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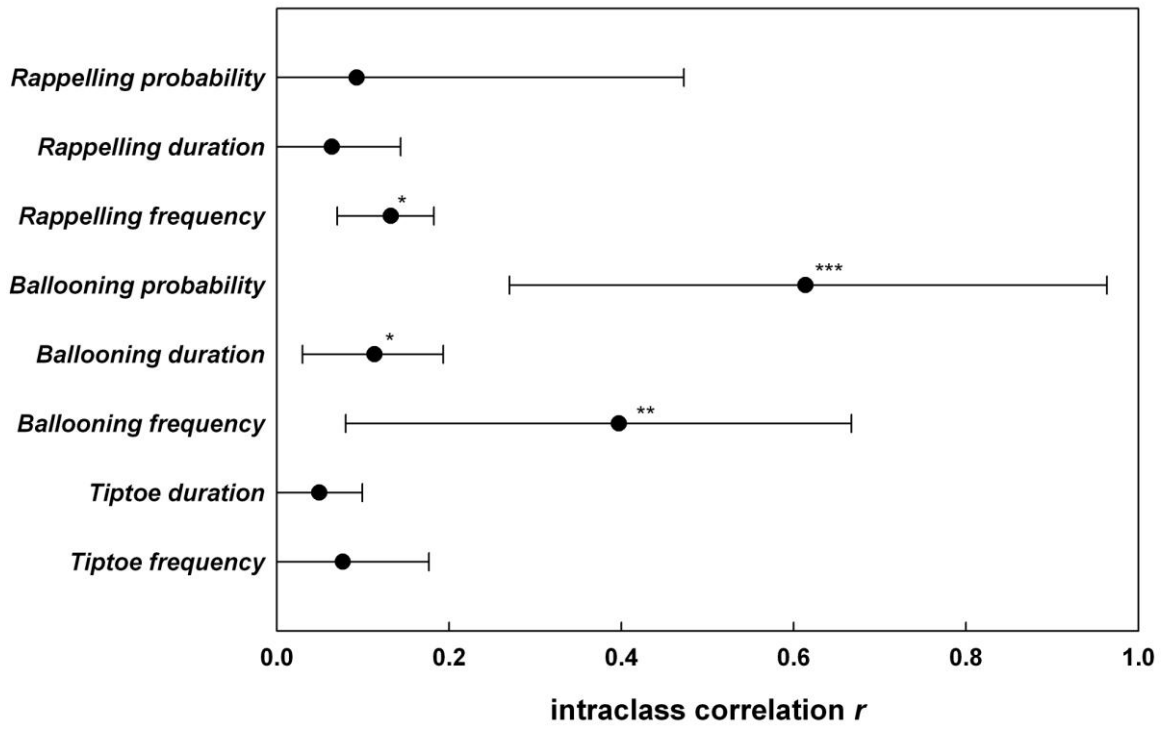| Behaviour	Consistency	SE
Tiptoe frequency	1.49	0.03
Tiptoe duration	1.08	0.06
Ballooning frequency	0.56	0.12
Ballooning duration	2.17	0.05
Rappelling frequency	0.74	0.07
Rappelling duration	1.75	0.04
Rappelling probability	0.68	0.03
Ballooning probability	0.79	0.02

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1 *Table 2. Test statistics of period (period prior or after the induction of the mating treatment) and mating*

2 *treatment (individuals either mated or not mated after period 1) on the different considered dispersal*

3 *behaviours. Slope gives the estimates of the separate regression of the behaviours on time (continuous*

4 *factor). Significance levels: ns: p>0.1; * < 0.1; ** < 0.5; *** < 0.01; **** < 0.001*

Factor	Period	mating	period*mating	Slope
Tiptoe duration	$F_{1,26.2}=12.91$ ****	$F_{1,35}=1.55$ ns	$F_{1,28}=1.80$ ns	-0.372 ± 0.117****
Tiptoe frequency	$F_{1,37.1}=17.40$ ****	$F_{1,59.1}=3.39$ *	$F_{1,45.6}=0.90$ ns	-0.048 ± 0.019***
Duration tiptoe before ballooning	$F_{1,22.8}=1.76$ ns	$F_{1,40.1}=1.85$ ns	$F_{1,24.8}=2.90$ ns	0.038 ± 0.284ns
Ballooning frequency	$F_{1,23.3}=6.62$ **	$F_{1,97.6}=1.08$ ns	$F_{1,34.5}=2.37$ ns	-0.094 ± 0.087* (unmated) 0.026 ± 0.034ns (mated)
Ballooning probability	$F_{1,41.6}=5.09$ **	$F_{1,48.2}=2.36$ ns	$F_{1,47}=2.94$ *	-0.140 ± 0.123* (unmated) 0.004 ± 0.049ns (mated)
Duration tiptoe before rappelling	$F_{1,52}=1.74$ ns	$F_{1,63}=2.18$ ns	$F_{1,63}=0.03$ ns	-1.313 ± 0.384ns
Rappelling frequency	$F_{1,31.8}=16.65$ ***	$F_{1,52.8}=3.14$ *	$F_{1,37.8}=0.12$ ns	-0.095 ± 0.026***
Rappelling probability	$F_{1,41.8}=5.09$ **	$F_{1,74.9}=4.09$ ns	$F_{1,74.8}=0.90$ ns	-0.142 ± 0.048***

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2 **Fig 1. Repeatability (mean intraclass correlation coefficient r and sᴇ) of the recorded tiptoe- and dispersal**

3 **behaviours. Behaviours marked with * show significant between-individual variation (*: P<0.05; **: P<0.01;**

4 ***: P<0.001)**

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