Heritability of dispersal in a rapidly spreading invasive spider

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Dispersal is an inseparable feature of animal life and a major determinant of species distributions and range dynamics. However, the role of the genetic architecture of dispersal behaviour, and hence the potential for its evolution in range-expanding species, is poorly understood. Here, we aimed to determine the heritability of dispersal behaviour for an invasive dwarf spider, Mermessus trilobatus, which has undergone rapid range expansion in Europe in the last few decades. Our results showed that spider dispersal traits were repeatable for the parental generation and heritable through both dam and sire. Behaviours were similarly heritable for female and male offspring. Interestingly, offspring of highly dispersive dams and sires exhibited almost three times higher dispersal propensity than offspring of at least one low-dispersive parent. The substantially high dispersal behaviour of the offspring of strictly highly vagile dams and sires indicates its recessive inheritance in this species. Recessive inheritance could favour invasiveness by facilitating high dispersal in inbred founder populations at the invasion front and returning to nonexaggerated mobility soon after an increase in genetic diversity.

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Dispersal is essential for adaptation and survival in new or changing environments (Hansson & Åkesson, 2014; Sheldon et al., 2017). It comprises all types of movements of animals and their propagules that result in increased gene flow across space (Ronce, 2007; Saastamoinen et al., 2018). Despite associated costs and risks (Bonte et al., 2012), dispersal can be favourable for species through lowering the density of kin, decreasing the rates of inbreeding and the probability of lineage extinction, and escaping pressures from natural enemies and conspecifics (Chuang & Peterson, 2016; Gandon, 1999; Lambin et al., 2001). Individual variation in dispersal can be explained by external factors (e.g. density dependence, habitat quality, inbreeding and outbreeding risks, kin competition, temperature during development) and internal state (e.g. behaviour, morphology, physiology; Bonte et al., 2008; Clobert et al., 2009; De Meester & Bonte, 2010). However, most studies focus on external factors as the main driving forces behind variation in individual dispersal behaviour. In contrast, the genetic background of dispersal behaviour and its role behind species distributions and range expansions are largely understudied (Bonte et al., 2018; Renault et al., 2018). Moreover, the available evidence is biased towards birds, insects and plants (Saastamoinen et al., 2018).

Range expansions could lead to spatial sorting whereby better dispersers accumulate in the areas close to the edge of the expanding range. At these low-density sites, highly vagile individuals often mate with each other resulting in dispersal-mediated spatial selection (Bonte et al., 2018; Shine et al., 2011). Owing to the variation in the offspring’s dispersal ability, the process could repeat by creating positive feedback loops manifesting in a continually expanding range (Bonte et al., 2018; Chuang & Peterson, 2016; Phillips et al., 2010a). One of the most intuitive causal mechanisms behind this accumulation of dispersive genotypes at the invasion front is the possible heritability of the dispersal traits across generations (Chuang & Peterson, 2016; Shine et al., 2011). Thus, if any dispersal component is heritable, then highly vagile parents will also produce highly dispersive offspring, leading to the ‘Olympic Village effect’ (Phillips et al., 2010a; Shine et al., 2011). A meta-analysis across 71 species by Dochtermann et al. (2019) showed that migratory/dispersal behaviours, defined as a single or repeated movement between areas during an organism’s life, are more heritable than other behavioural and life
history traits and physiological responses. Although the analysis showed no difference in heritability estimates between vertebrates and invertebrates, the data set was taxonomically biased (83% from vertebrates; Dochterman et al., 2019), indicating a lack of research in invertebrate trait heritability.

Evolutionary drivers of behaviour can differ between the sexes, often leading to behavioural differences between males and females (reviewed in Schuett et al., 2010). Correspondingly, the heritability of behavioural traits can also be sex specific (e.g. Han & Dingemanse, 2017; Kralj-Fiser et al., 2019; Li & Kokko, 2019; Saastamoinen, 2008; Yip et al., 2021). Sex-specific heritability of dispersal might play an important role in the dynamics of range expansion (Trochet et al., 2016). For example, inheritance of the often higher dispersal in males than females would contribute little to range expansions and could even reduce expansion velocity at the range fronts (Miller & Inouye, 2013). By contrast, high female dispersal could accelerate the spread, particularly if fertilized females are capable of long-distance dispersal (Van Wingerden, 1980; Weyman et al., 2002). This is the case in dwarf spiders (Araneae: Linyphiidae; Weyman et al., 2002), which are the numerically dominant spider family in temperate to cold climates (Coddington & Levi, 1991).

Biological invasions play an increasing role in global biodiversity patterns (Simberloff et al., 2013). Non-native species are considered invasive when they successfully establish and rapidly spread in their exotic range by overcoming novel ecological pressures (Blackburn et al., 2011; Sakai et al., 2001). Since the role of dispersal is central in range expansions, the phenotypic variation in individual dispersal ability may accelerate or limit biological invasions (Renault et al., 2018). Therefore, dispersal behaviour and hence the heritability of high dispersal, including sex-specific inheritance, could play an essential role in invasion success.

Despite the growing impact of invasive species on ecosystems and human welfare (Mooney, 2005; Pimentel et al., 2005), invasions by spiders have only recently started to attract scientific attention (Campbell et al., 2020; Chuang & Riechert, 2021; Mowery et al. 2021; Narimanov, Kempel et al., 2021; Nentwig, 2015). *Messus trilobatus* (Araneae: Linyphiidae; formerly known as *Eperigone trilobata*) is a North American dwarf spider (Millidge, 1987) that was first recorded in Europe in the late 1970s in southwest Germany (Dumpton & Platen, 1985). The species has undergone a rapid spread in Europe (Hirna, 2017), expanding its range by more than 1000 km in 50 years. These small spiders (1.6–2.1 mm) live among vegetation close to the ground surface (Nentwig et al., 2021) and frequently engage in aerial dispersal (Blandenier, 2009).

Spiders disperse over long distances via ‘ballooning’, where individuals release threads of silk in the air from their spinnerets and become airborne with the aid of meteorological forces (Bell et al., 2005; Weyman, 1993). Dispersal over a short distance is called ‘rappelling’ when the thread attaches to a nearby object and is then used by the spider to walk along (Bonte et al., 2009). Before ballooning or rappelling, spiders show motivation to disperse by performing predispersal behaviour. *Messus trilobatus* often performs two types of predispersal behaviour. First, when spiders tip toe, they release strands of silk in the air by straightening their legs and lifting their abdomens (Eberhard, 1987). Second, spiders perform ‘rafting’ when they attach the silk threads to elevated positions and slide down on these threads. They use the silken lines as platforms to take off once the meteorological factors are strong enough to lift the spiders (Bell et al., 2005; Tolbert, 1977). Predispersal behaviour is important for ecological and evolutionary studies since it indicates spiders’ willingness to disperse (Weyman, 1993; but see Lubin & Suter, 2013).

The invasion success of *M. trilobatus* in Europe is not explained by a ruderal strategy (Narimanov, Kempel et al., 2021), competition with native sympatric species (Eichenberger et al., 2009) or release from a generalist predator (Narimanov, Hatamlı et al., 2021). Nevertheless, *M. trilobatus* often reach high local abundances in grasslands (Narimanov, Kempel et al., 2021; Schmidt et al., 2008) and have colonized a major part of Europe in a relatively short time (Hirna, 2017). Therefore, the heritability of dispersal might play an essential role in their spread and colonization success in Europe in less than 50 years. Although several empirical studies report the heritability of dispersal in spiders (e.g. Bonte & Lens, 2007; Yip et al., 2021), it has, to our knowledge, never been studied in an invasion context.

In this study, we investigated the heritability of dispersal traits, namely tip toe, rafting and take-off, for *M. trilobatus*. With the aid of repeated dispersal experiments across two generations, we sought to determine: (1) whether the dispersal traits are inherited through the dam and/or sire; and (2) if heritable, whether dispersal traits of offspring are inherited sex specifically.

**METHODS**

**Study Species and Generations**

We sampled spiders from two distant locations to capture high genetic variability: around Vienna in Austria and Landau in Germany, approximately 600 and 50 km from the presumed core (Dumpton & Platen, 1985) and 560 and 1200 km from the current front (Hirna, 2017) of the invaded range, respectively. Offspring from Vienna showed a similar dispersal propensity to their counterparts from Landau (negative binomial generalized linear models: P > 0.3). Sampling was done in June and July in 2020 using a vacuum sampler (modified StiHL SH46 blower; Stihl, Waiblingen, Germany). In total, we sampled 26 females in Vienna and 28 in Landau from six different hay meadows in each location. Only mated females (F0) were sampled and identified by the presence of a mating plug (Fig. 1). The plug is developed after the first mating and covers the epigyne (Fig. 1a and b) to secure paternity (Uhl et al., 2010). Thus, while males of *M. trilobatus* (Fig. 1c) can mate several times in their lives, females are monandrous. We treated perennial hay meadows as the preferred type of habitat of *M. trilobatus* in Europe (Narimanov, Kempel, et al., 2021). All spiders were transferred individually into glass jars (405 ml) with a 1 cm layer of plaster of Paris to ensure high humidity inside the glasses. We kept all individuals in climate cabinets under standard conditions (25 °C, relative humidity = ca. 65%, 16:8 h light:dark) to obtain a high number of egg sacs. Each female produced multiple egg sacs, and we were able to obtain at least 500 offspring. To minimize stress during development and thus ensure basic dispersal levels when adult (De Meester and Bonte, 2010; Mestre & Bonte, 2012), we fed all spiders ad libitum with springtails, *Sinella curviseta*, and separated the next generation of spiderlings (F1). We transferred all F1 offspring individually into 30 ml glass jars with a layer of humid plaster on the bottom and fed them ad libitum until adulthood. The second generation of spiders (F2) was reared in a similar manner.

**Ethical Note**

We kept spiders under the conditions described above to ensure the welfare of these animals. The spiders were separated from siblings at the early stage of development and kept individually in glass jars with enough space for web building, which resulted in a high survival rate (> 90%). Almost all spiders successfully mated and produced offspring. After experiments, spiders sampled in Landau and their offspring were released to fields around Landau when possible. Spiders originating from Vienna were euthanized at −20 °C.
Dispersal Experiment

The spiders’ propensity for aerial dispersal was tested in an arena (shown in Appendix Fig. A1a). To provide a suitable airflow of 1 m/s (± 0.1) for dispersal (Entling et al., 2011), we placed a table fan (diameter = 10 cm, 2.5 W) approximately 0.8 m beside the arena. We measured wind velocity at the position of the arena using a hot-wire anemometer (VOLTCRAFT PL-135). The experimental arena was shielded from ambient electric fields to reduce the potential influence of atmospheric electric fields on spiders’ dispersal behaviour (Narimanov, Bonte, et al., 2021). We used an experimental frame consisting of two metal electrodes (0.8 × 0.8 m²) held parallel to each other and 0.8 m apart. The interconnected electrodes were electrically grounded. A dispersal platform was placed in the middle of the lower electrode (Appendix Fig. A1a). This consisted of a disk of plaster of Paris with a 2.5 cm diameter and a 7 cm tall wooden stick in the middle to provide an elevated position for take-off (Appendix Fig. A1b). We prevented spiders from walking out of the arena by placing the platforms in the middle of petri dishes filled with water. We used a vertically oriented textile mesh 1.5–2 m downwind from the arena to capture dispersing spiders.

We tested each spider three times on consecutive days (one trial a day). In each trial, we placed a spider on the dispersal platform and observed its behaviour. The trial was ended after 10 min or once the spider took off. We washed and wiped the platforms with water between the trials to remove the silk and possible chemical cues left by the previous spider. To increase the likelihood of dispersal (Weyman et al., 1994), we starved all individuals for 3 days before the experiment. We recorded the frequency of tiptoe, rafting and take-off. The behaviour was analysed blind to spiders’ previous performance, their IDs and groups. We tested 425 adult F1 individuals in total (212 females and 213 males).

Breeding Design

We assigned 26 F1 spiders (15 females and 11 males) with the highest predispersal propensity (at least one tiptoe or rafting event in each of three trials) to a high-dispersive group and 30 F1 individuals (19 females and 11 males) with no predispersal behaviour to a low-dispersive group to establish groups for high and low dispersal, respectively. We mated high- and low-dispersive individuals randomly (also including crossed pairs originating from Vienna and Landau), avoiding direct inbreeding and resulting in a set of 34 F1 female broods: seven high-high (HH); eight high-low (HL); 11 low-high (LH); eight low-low (LL; the first letters stand for dams’ and the second letters for sires’ dispersive groups). We kept individuals under standard conditions (25 °C, relative humidity = ca. 65%, 16:8 h light:dark) and fed them ad libitum to obtain the F2 generation. We reared 477 F2 offspring in total (for sample sizes, see Appendix Table A1). To demonstrate the heritability of dispersal propensity and to determine the role of dam and sire heritability, we carried out the dispersal experiment three times with each F2 individual during 3 consecutive days as described above.

Figure 1. (a) A virgin female, (b) a mated female with a plug and (c) a male of Mermessus trilobatus. The photos were taken with a LEICA 5Xi stereo microscope with an integrated 10 MP CMOS-camera.

Statistical Analysis

All analyses were performed in R 4.0.3 (R Core Team, 2021).

Repeatability

The portion of the variation in behaviour that is due to between-individual differences is expressed as the repeatability of this trait. Thus, behaviour is considered repeatable when between-individual variance is higher than within-individual variance and consistent through time (Bell et al., 2009; Hayes & Jenkins, 1997). Consequently, high repeatability of behaviour indicates that the individuals differ from each other in their behaviours. Therefore, we estimated the repeatability of tiptoe, rafting and take-off behaviours for the parental generation (F1) by using the rpt function with binomial distribution from the rptR package (Stoffel et al., 2017) with 1000 permutations. We included F1 spiders’ sex as a fixed predictor and calculated adjusted repeatability (Radj) with 95% confidence intervals as the appropriate parameter for the models including fixed effects (Nakagawa & Schielzeth, 2010). We used only repeatable traits as a proxy for dispersal ability.

Heritability

To investigate the role of dam and sire heritability in dispersal behaviour of the offspring generation (F2), we modelled the frequency of tiptoe, rafting and take-off by fitting negative binomial generalized linear models (glm.nb) from the MASS package (Venables & Ripley, 2002). We included F1 dam and sire dispersive groups (factor of two: High and Low), offspring sex and all interaction terms (dam*sire; dam*sex; sire*sex; dam*sire*sex) as fixed predictors. We determined the role of the dam and/or sire and the possible sex-specific heritability using the Anova function (chisquare test) from the R package car (Fox & Weisberg, 2019). To determine the portion of the variation in behaviour explained by dam and sire components, we calculated the variance of dam and sire
sire dispersive groups using negative binomial generalized linear mixed-effects models (glmer.nb) from the lme4 package (Bates et al., 2015). We used a negative binomial distribution as the most flexible and appropriate for the count data (O’Hara & Kotze, 2010). We also used the Games–Howell post hoc test to illustrate the difference between the breeding groups’ performance (HH, HL, LH, LL) by using the games-howell-test function from the rstatix package (Kassambara, 2020).

RESULTS

Repeatability

Tiptoe, rafting and take-off behaviours of spiders from the parental generation (F₁) were repeatable at the individual level (Fig. 2, Appendix Table A2). Calculated 95% confidence intervals for all measured behaviours did not overlap with 0 (Fig. 2). These repeatability scores are in line with the values found in the literature (average repeatability in behaviours of 98 species across eight taxa: 0.37; Bell et al., 2009) and can be considered moderate. Consequently, we used all three traits in subsequent analyses.

Heritability

Spiders’ tiptoe, rafting and take-off behaviours were largely heritable through dam and sire. Interestingly, on average, offspring of only high-dispersive dams and sires (group HH) showed an approximately three times higher frequency for tiptoe, rafting and take-off than offspring of at least one low-dispersive parent (groups HL, LH and LL; Table 1, Fig. 3). Offspring of a vagile dam or sire showed at least twice as much tiptoe, rafting and take-off propensity as offspring of the respective low-dispersive parent (Fig. 4). The additive genetic components (dam + sire) explained 33, 41 and 38% of the variation in tiptoe, rafting and take-off behaviour of the offspring generation, respectively (Fig. 5, Table 2). The sire components explained twice as much variation in tiptoe as dam components, whereas the difference was only slightly biased towards sire components in the offspring’s take-off behaviour. In rafting, the dam and sire components similarly explained the variation in behaviour (Fig. 5, Table 2). We found no evidence for sex-specific heritability of any trait (Table 1). Overall, males showed higher frequencies of rafting and take-off than females but a similar frequency of tiptoe behaviour (Table 1).

DISCUSSION

External factors and individual internal states, including the genetic prerequisites, are drivers of individual variation in dispersal. Although numerous studies have investigated external factors as the main forces behind individual dispersal behaviour, little is known about the role of the genetic background of dispersal and its heritability in species’ range dynamics (Bonte et al., 2018; Renault et al., 2018). Here, we found high heritability of dispersal behaviour of a highly invasive spider, M. trilobatus. The dispersal behaviour of M. trilobatus was heritable through both dam and sire and similarly heritable for both female and male offspring.

The additive genetic components (dam + sire) explained on average 37% of the variation in offspring dispersal behaviour. The values calculated here are in line with values found in the literature (Docterman et al., 2019). Dispersal (distance moved) has been proven heritable for invasive cane toads, Rhinella marina, which have rapidly expanded their range in Australia (Phillips et al., 2010b). However, in contrast to M. trilobatus, the toads were introduced en masse (Lever, 2001), and hence high genetic variability was expected. Further, our results showed that on average 63% of the variance in behaviours was unexplained by additive genetic components. We assume that this unexplained variation was largely random since all spiders were kept under standard conditions and separated from siblings at an early stage of development.

Besides genetic background, external factors, such as temperature during development (Bonte et al., 2008) or density dependence of dispersal (De Meester & Bonte, 2010), might also affect the dynamics of range expansions. Consequently, a high dispersal and/or plasticity in dispersal behaviour based on individual development (e.g. temperature, population density) could make species equally prone to accelerated range expansions without the genetic predisposition of dispersal. Furthermore, the variability in dispersal behaviour can also be explained by the interplay of genetic and external factors (e.g. wind*sire components in dispersal motivation of the lycosid spider Pardosa purbeckensis; Bonte & Lens, 2007).

Interestingly, only offspring of both high-dispersive dams and sires (HH group) had substantially higher tiptoe, rafting and take-off propensity than the offspring with at least one low-dispersive parent (HL, LH and LL groups). The pattern was similar for both sexes. This indicates that high dispersal is inherited recessively and present in offspring in which strictly both parents were highly dispersive. We expect high dispersal, if inherited recessively, to be suppressed in dense, stable populations. In contrast, at low-density

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Table 1: Outputs for logistic regression models predicting the frequency of tiptoe, rafting and take-off behaviour of the offspring generation (F₂).

| Behaviour | χ² | P   | χ² | P   | χ² | P   |
|-----------|----|-----|----|-----|----|-----|
| Tiptoe    |    |     |    |     |    |     |
| Rafting   |    |     |    |     |    |     |
| Take-off  |    |     |    |     |    |     |
| Dam       | 18.89 | <0.0001 | 50.70 | <0.0001 | 22.24 | <0.0001 |
| Sire      | 39.37 | <0.0001 | 53.28 | <0.0001 | 32.94 | <0.0001 |
| Dam*Sire  | 5.40 | 0.02 | 8.95 | 0.003 | 6.58 | 0.01 |
| Sex       | 1.77 | 0.183 | 9.20 | 0.002 | 8.09 | 0.005 |
| Dam*Sex   | 0.08 | 0.776 | 0.01 | 0.913 | 0.08 | 0.783 |
| Sire*Sex  | 0.99 | 0.321 | 0.73 | 0.392 | 2.15 | 0.143 |
| Dam*Sire*Sex | 0.38 | 0.540 | 0.13 | 0.721 | 0.05 | 0.825 |

The models predict frequency of behaviours considering the dispersive groups of dam and sire (High; Low), offspring sex and all interaction terms (dam*sire; dam-*sex; sire*sex; dam*sire*sex). Significant correlations are shown in bold.

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Figure 2: Adjusted repeatability (Radj) and 95% confident intervals of tiptoe, rafting and take-off frequencies of spiders from the parental generation (F₁). The dashed line represents 0. See Appendix Table A2 for P values.
Figure 3. Effect of the parents’ (F1) dispersal ability on (a) tiptoe, (b) rafting and (c) take-off behaviour of the offspring generation based on their breeding groups (F2; HH: high-dispersive parents; HL: high-dispersive dam and low-dispersive sire; LH: low-dispersive dam and high-dispersive sire; LL: low-dispersive parents). Means ± SE are presented. Differences between the groups are illustrated with letters based on the results from a Games-Howell post hoc test.

Figure 4. Frequency of (a, d) tiptoe, (b, e) rafting and (c, f) take-off behaviour based on (a, b, c) dam and (d, e, f) sire dispersive groups (High: high-dispersive; Low: low-dispersive). Means ± SE are presented.
Dispersal behaviour of *M. trilobatus* was similarly heritable for females and males. However, female-biased, sex-specific heritability of tiptoe behaviour was recently revealed in a colonial spider, *Cyrtauchena citricola*. Despite similar behaviour in both sexes, genetic variance contributed to the between-individual variation of tiptoe behaviour only in females (Yip et al., 2021). In contrast to *M. trilobatus*, *C. citricola* are mainly colonial spiders (Kullmann, 1959; Mestre & Lubin, 2011). In group-living spiders, females are often under selection for successful dispersal and establishment of new colonies (Berger-Tal et al., 2016; Lubin et al., 2009; Lubin & Bilde, 2007). In such group-living spiders, males may be less affected by selection, have more plastic strategies or alternatively be selected against high dispersal to maintain group cohesion. However, note that the populations tested in the study by Yip et al. (2021) were in their native range, and sex biases in dispersal heritability may largely affect the evolutionary dynamics of species’ range expansions in populations in non-native ranges (e.g. in North America for *C. citricola*; Chuang & Riechert, 2021). Further, in solitary *M. trilobatus*, the heritability of dispersal behaviour for both sexes might also explain their rapid spread in Europe in a relatively short period. Subsequently, along with highly dispersing female offspring of highly vagile parents, highly dispersive male offspring could quickly reach low-density sites and hence lower the risk of mate limitation and increase genetic diversity. However, note that in some female-biased dispersal systems, male genetic material can also disperse passively via females after successful mating (Lubin & Bilde, 2007).

The heritability of dispersal behaviour of *M. trilobatus* through both dam and sire could explain their rapid spread and colonization success in Europe. The species has undergone rapid range expansion in less than 50 years after it was first recorded in Germany (Dumpert & Platen, 1985; Hirna, 2017). Therefore, highly vagile individuals in the vanguard of their expanding range could mate at low-density sites and produce equivalently dispersive offspring leading to the accumulation of dispersive genotypes at the dynamic edge of this range (Bonte et al., 2018; Shire et al., 2011). Further, note that the dispersal propensity of *M. trilobatus* was approximately four times lower during the laboratory experiment than in native linyphiid species, namely *Agyneta rurestris* and *Erigone dentipalpis* (Narimanov, Bonte et al., 2021). Hence, as dispersal is risky (Bonte et al., 2012), low dispersal could be advantageous in stable populations, whereas the recessive inheritance of high dispersal behaviour could boost vagility at the front of their expanding range. Consequently, the range of *M. trilobatus* in Europe might be spatially sorted with an accumulation of highly dispersive individuals at the front. Nevertheless, accelerated range expansions can also rapidly break off once the less dispersive individuals reach remote areas and mix with high dispersers (Chuang & Peterson, 2016). The phenotypic shift through space in voracity and exploration has been recently demonstrated for an invasive spider in the United States (Chuang & Riechert, 2021). However, the possible spatial sorting of invasive *M. trilobatus* in Europe requires further investigation.

**Conclusion**

The higher dispersal ability of the offspring from two high-dispersive parents compared to offspring of at least one low-dispersive parent indicates recessive inheritance of high dispersal in *M. trilobatus*. Further, the heritability of dispersal in invasive *M. trilobatus* implies the potential of selection for high dispersal at the invasion front of their expanding range. Thus, studies investigating the dispersal behaviour of spiders from the populations close to the edge and the core of the invasion range are needed to better understand the spatial distribution and the rapid spread of invasive *M. trilobatus* in Europe.
Author Contributions

Nijat Narimanov: Methodology (equal); Formal analysis (lead); Investigation (lead); Data curation (lead); Writing—original draft (lead); Visualization (lead); Project administration (lead).

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Data Availability

Data generated and analysed during this study are available from Figsdate: https://doi.org/10.6084/m9.figshare.8614836.v1.

Declaration of Interest

The authors have no interest to declare.

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Table A1

| Group | Females | Males | Total |
|-------|---------|-------|-------|
| HH    | 50      | 62    | 112   |
| HL    | 54      | 55    | 109   |
| LH    | 61      | 71    | 132   |
| LL    | 65      | 59    | 124   |
| Total | 230     | 247   | 477   |

HH: high-dispersive parents; HL: low-dispersive parents and high-dispersive sire; LH: low-dispersive dam and high-dispersive sire; LL: low-dispersive parents.

Table A2

| Dispersal traits | R  | SE  | CI  | P   |
|------------------|----|-----|-----|-----|
| Tipoff           | 0.362 | 0.07 | 0.287; 0.585 | <0.0001 |
| Kating           | 0.297 | 0.036 | 0.206; 0.344 | <0.0001 |
| Take-off         | 0.287 | 0.095 | 0.217; 0.61 | <0.0001 |

The individual behaviours were tested three times on consecutive days. CI: confidence interval. Significant correlations are shown in bold.
Figure A1. (a) Side view to the experimental set-up comprising the experimental frame with two interconnected and electrically grounded parallel metal electrodes, a table fan and a mesh to capture spiders. (b) Dispersal platform with a vertical stick made of moist plaster of Paris and connected to the bottom electrode via a wire.