

Contrasted propensity for waterborne and airborne dispersal between two closely related semi-aquatic spider species

Jérémy Monsimet¹  | Julien Pétilon^{2,3}  | Olivier Devineau¹  | Nino Gardoni¹ | Léa Bataillard¹ | Denis Lafage^{2,4} 

¹Department of Forestry and Wildlife management, Inland Norway University of Applied Sciences, Campus Evenstad, Koppang, Norway

²University of Rennes, CNRS, ECOBIO (Ecosystèmes, biodiversité, évolution) - UMR 6553, Rennes, France

³Institute for Coastal and Marine Research, Nelson Mandela University, Port Elizabeth, South Africa

⁴Department of Environmental and Life Sciences/Biology, Karlstad University, Karlstad, Sweden

Correspondence

Jérémy Monsimet, Department of Forestry and Wildlife management, Inland Norway University of Applied Sciences, Campus Evenstad, Koppang, Norway.
Email: jeremy.monsimet@posteo.net

Editor: Christopher Hassall

Associate Editor: Myles Menz

Abstract

1. Dispersal abilities are important to support metapopulation functioning and species distributions, yet it is rarely accounted for in conservation. Here, we compared the propensity for dispersal between the two fishing spiders present in Europe: the widespread habitat-generalist *Dolomedes fimbriatus* and the scarcer red-listed *Dolomedes plantarius*.
2. We experimentally tested for airborne and waterborne dispersal using first instar juveniles sampled in nursery webs, and older juveniles. We estimated the propensity for short and long-distance dispersal of airborne and waterborne behaviours, and we tested the difference between species with generalised linear mixed models.
3. Airborne (ballooning) and waterborne (sailing) behaviours were more frequent for *D. fimbriatus* than for *D. plantarius*, indicating a higher propensity of the former for long-distance dispersal.
4. The frequency of rappelling behaviour, and thus the propensity for short-distance dispersal, did not differ between species. However, we found contrasting results for short-distance dispersal on the water, with rowing being more frequent and running less frequent for *D. plantarius* than for *D. fimbriatus*.
5. The different propensity for dispersal between the two species might be partly explained by the ecology of *D. plantarius*, which is known to be more habitat-specialist and more dependent to water bodies than *D. fimbriatus*.
6. The limited propensity for dispersal of the red-listed *D. plantarius* is another argument for conserving an interconnected network of wetlands in Fennoscandia. Indeed, increased isolation of populations would be detrimental for species maintenance.

KEYWORDS

dispersal behaviours, generalist species, long-distance dispersal, Pisauridae, short-distance dispersal, specialist species

INTRODUCTION

Dispersal is a crucial process to support gene flow between spatially structured populations (Ronce, 2007). It also plays a key role to sustain

population genetics and species distributions. Therefore, dispersal has a major influence in the response of species to climate changes (Travis et al., 2013). Indeed, a northward expansion is expected for species in the northern hemisphere (Parmesan & Yohe, 2003; Sturm et al., 2001),

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Insect Conservation and Diversity* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society.

but species require long-distance dispersal abilities to expand their range (Trakhtenbrot et al., 2005). However, few species are plastic enough to cope with climate change by adapting their physiology or their life-history (Radchuk et al., 2019).

There are two types of dispersal, active and passive, which are defined by the three stages of emigration (initiation of the movement to leave a habitat), transfer (movement per se) and immigration (end of the movement, settlement in a novel habitat) (Clobert et al., 2009). In active dispersal, organisms control their own locomotion, whereas in passive dispersal, they depend on external factors (e.g. other animals, wind, water current, etc). Both types of dispersal have a cost (reviewed by Bonte et al., 2012). Habitat quality (Bonte, Lens, et al., 2003) and connectivity (Baguette & Van Dyck, 2007; Van Dyck & Baguette, 2005), as well as intraspecific factors such as sex-ratio (Trochet et al., 2016) all influence the prevalence of dispersal and make it highly context (e.g. taxon and site) dependent.

Because of its importance in sustaining populations, understanding the dispersal of species of interest is fundamental for conservation purposes. Among the 102 fishing spiders known to date (World Spider Catalog, 2022), we focused on the dispersal of the two European species. They both inhabit wetlands, which are threatened by land-use change due to expansion of agriculture or urbanisation (Davidson, 2014). *Dolomedes plantarius* (Clerck, 1757) and *Dolomedes fimbriatus* (Clerck, 1757) are both widely distributed in Europe, but the former has scarcer populations and is red-listed as vulnerable at the European scale. Indeed, Vugdelić (2006) observed in the United Kingdom that two populations of *D. plantarius* distant by less than a kilometre from each other were genetically isolated. Regarding their habitat requirements, *D. plantarius* is less habitat generalist and is limited to more open habitat, fenlands or riverbanks with a constant presence of water (Dickel et al., 2022; van Helsdingen, 1993). *D. fimbriatus* is more tolerant to more oligotrophic wetlands with lower pH and is less dependent to water. Because *D. fimbriatus* is more generalist, both species can co-exist in a site that would be more of a *D. plantarius* site.

Spiders display a broad range of dispersal modes, which can occur by air, water, or on the ground. As such, they make a good model to study dispersal: short-distance dispersal is usually active, whereas long-distance dispersal is usually passive. Small spiders and young first instars, the so-called spiderlings, are able to disperse through the air (Bell et al., 2005). The tiptoeing behaviour is widely studied as a proxy for any silk-related dispersal, such as ballooning or rappelling (Bonte, Travis, et al., 2008; Bonte, Vandenbroecke, et al., 2003; Frost et al., 2013; Goodacre et al., 2009; Pétilion et al., 2012; Woolley et al., 2007). Ballooning is a passive behaviour that has evolved from an ancestral 'suspended ballooning' towards the ballooning behaviour (Bell et al., 2005), where spiders take off from a tiptoeing position to travel from some hundred metres to some kilometres throughout the air (Thomas et al., 2003). Furthermore, spiders can travel shorter distances by means of rappelling, using silk as a bridge between plant stems. Rappelling is mainly present in small spiders like Lynphiidae (Bonte et al., 2009), or at younger and smaller stages. Because *Dolomedes* are semi-aquatic, they are also able to disperse on the water. Behaviours on water have been well described for *Dolomedes triton*

(Suter, 1999, 2013; Suter et al., 1997; Suter & Gruenwald, 2000; Suter & Wildman, 1999), a fishing spider species presents in North America. Moreover, Hayashi et al. (2015) showed that aerial dispersal abilities are usually correlated with dispersal abilities on water. Furthermore, Suter (1999) hypothesised that sailing, a passive behaviour of spiders raising legs, body, or abdomen to catch the wind and travel at low cost, could be considered as ballooning for waterborne dispersal. Active movements on water can be characterised by three distinct active behaviours: walking, rowing and running (Suter, 2013).

Ballooning is a passive and largely uncontrolled behaviour, which is partly heritable (Bonte & Lens, 2007), and influenced by context and information accumulated over long time (Bonte et al., 2009). Consequently, no fast decisions but more pro-active strategies (genetically inherited or not) are the only solution to experience benefits of long distance (uncontrolled) dispersal. We expected sailing to be less uncontrolled than ballooning as patches of populations distributed along continuous stream or water bodies are more predictable than for long-distance airborne dispersal. Rappelling is an important mode of dispersion for spiderlings. It is a more controlled behaviour, which can be used for short-distance dispersal based on direct information from the local habitat (Bonte et al., 2009), as well as to escape predation or kin selection. Similarly, rowing and running, used by bigger and older juveniles (Suter & Wildman, 1999), would illustrate short-distance dispersal or movement within populations to escape competition with others, or a response to immediate stress in the habitat.

We expected that the wider range of suitable habitats of *D. fimbriatus* would correspond to a greater propensity for long-distance dispersal. Indeed, chances to arrive in a suitable habitat are higher than for *D. plantarius*. Such hypothesis has already been formulated by Duffey (2012) based on his observations in the wild. We also hypothesised that *D. plantarius*, due to its higher dependency to water, has a higher propensity for short-distance dispersal on the water than *D. fimbriatus*. These movement behaviours on water likely reflect the ecology of both species and we hypothesised that *D. plantarius*, which is more dependent on water, is more likely to efficiently move on water than *D. fimbriatus*. We did not expect differences between species in the propensity to rappel, because we tested spiderlings individually, under similar competition pressure.

MATERIALS AND METHODS

Study species

Both European fishing spider species are widespread in Europe. *D. plantarius* has lower population densities and is red-listed (Baillie et al., 1996). Both species have relatively similar lifecycles. Females lay their eggs into a large silk eggsac, which they carry for about a month before building a nursery in the vegetation. Spiderlings hatch in the nursery and stay there for about a week while the mother stands guard. Spiders usually require about 2 years to reach maturity, but it varies from one to three or even more (Duffey, 2012). Moreover, *D. fimbriatus* is less restricted by the absence of water, except when females carry

their eggsacs, which must be dipped into water to keep the eggs moist. *D. plantarius* is more dependent to the presence of water in the site than *D. fimbriatus* (Dickel et al., 2022; Duffey, 2012).

Spider sampling

To test the propensity for airborne dispersal of spiders, we sampled spiderlings directly from the nursery web, by gently opening it with tweezers and sucking up about 10 spiderlings with an insect aspirator. We used the ‘sponge-box’ technique on the female guarding the nursery to identify the species. The female was gently pressed between a sponge and the bottom of the box to inspect her epigyne (see Dickel et al., 2022 for detailed technique). We sampled 11 sites in July/August 2019 (See Figure S1 in Appendix 1). To test the difference between species, we sampled two sites with *D. fimbriatus* (Df1 and Df2), two sites with *D. plantarius* (Dp1 and Dp2) and one site with both species (Bs1) in southern Sweden. We sampled two sites with each species and two sites with both species in central Sweden (Df3 and Df4; Dp3 and Dp4; Bs2 and Bs3, respectively). The number of spiderlings tested per nursery and per site is presented in Table 1.

To test the propensity for waterborne dispersal of spiders, we sampled older juveniles (called juveniles in the following) from seven sites (see Figure S1 in Appendix 1). We used older spiders than for airborne dispersal to be able to see short-distance dispersal on the water, which is more constrained by hydrodynamics in smaller *Dolomedes* (Suter & Wildman, 1999). In order to test the difference between species, we sampled two sites with *D. fimbriatus* (Df1 and Df2) and one site with *D. plantarius* (Dp2) in southern Sweden and two sites with each species in central Sweden (Bs3 and Df4; Dp3 and Dp4). The number of juveniles tested per sites is presented in Table 1.

Dispersal experiments

Propensity for airborne dispersal

Before the test, we kept the spiderlings for 6 days in individual vials with a water-saturated cotton ball, at constant 20 °C, 12:12 hours light:dark conditions. They were fed with one fruit fly (*Drosophila melanogaster*) on the day of capture to control for the impact of starvation on ballooning (Bonte, Lukáč, et al., 2008; Bonte, Travis et al., 2008).

We tested propensity for airborne dispersal of spiders with a platform (10 × 10 cm) with vertical wooden sticks (approximately 20 cm height) arranged in two rows. The platform was surrounded with water to prevent escape. A fan was used to simulate an upward wind at a velocity of 1.0 m/s, which Frost et al. (2013) identified as a favourable speed to observe dispersal behaviours in *Dolomedes triton*. Each spider was tested individually for up to 10 min, during which it was put back on the platform after each dispersal event, although a few individuals were lost or died during the first trial. We left spiders moving along silk threads to see whether spiders dropping from a silk would either use the silk to rappel or balloon. We removed silk from the platform with a brush after each

TABLE 1 Number of juveniles and spiderlings sampled and tested in the different sites (see Figure S1 in Appendix 1 for the location of the sampling sites)

Site	Species	Number of juveniles	Number of spiderlings/nursery
Bs1	<i>D. fimbriatus</i>	0	10/9/9
Bs2	<i>D. fimbriatus</i>	0	10/8/10
Bs2	<i>D. plantarius</i>	0	6/7/9
Bs3	<i>D. fimbriatus</i>	27	8/10/6
Bs3	<i>D. plantarius</i>	0	5/8
Df1	<i>D. fimbriatus</i>	11	8/10/6
Df2	<i>D. fimbriatus</i>	10	10/10/10
Df3	<i>D. fimbriatus</i>	0	8/10/8
Df4	<i>D. fimbriatus</i>	29	9/6/8
Dp1	<i>D. plantarius</i>	0	9/8/10
Dp2	<i>D. plantarius</i>	11	8/8/6
Dp3	<i>D. plantarius</i>	28	4/6/6
Dp4	<i>D. plantarius</i>	27	4/9/9

spiderling, to avoid that the presence of another spider’s silk affected the frequency of aerial dispersal (see De Meester & Bonte, 2010). After these experiments, we released the spiders back into their site of origin.

We live-recorded the spiderlings’ behaviours with software BORIS (Friard & Gamba, 2016). We measured the number of occurrences and duration of ballooning, as a proxy for long-distance dispersal; rappelling, as a proxy for short-distance dispersal; tiptoeing and climbing, which we later excluded from the analysis of dispersal (see Table S1 in Appendix 3).

Propensity for waterborne dispersal

Before the test, we kept the juveniles for 7 days in individual vials with a water-saturated cotton ball, at constant 20 °C, 12:12 hours light:dark conditions. They were fed with one fruit fly (*D. melanogaster*) on the day of capture to control for the impact of starvation.

We placed the juvenile spiders on the water in the middle of an aquarium. Behaviours of spiders were observed from the release of the spider to the moment the spider either crossed the ‘goal line’, climbed a wall/window, or reached a platform (see Figure S2 in Appendix 2 for details on the experimental design). Spiders were tested for three water current speeds (0, 1 and 2 m/s) and three wind speeds (0, 1.5 and 2.5 m/s). Each spider was tested three times at one of the wind/water speed combination, to control for potential acclimatisation to the aquarium. Experiments were carried out using fresh water at a temperature of 15 °C. We weighted each spider after the experiment to control for a possible effect of the weight on propensity for waterborne dispersal. After these experiments, we released the spiders back into their site of origin.

Spider behaviours were recorded live with a camera, and later analysed with software BORIS (Friard & Gamba, 2016). The different behaviours on the water surface were sailing (with legs,

abdomen or by raising the body), considered as a proxy of long-distance dispersal; rowing, walking and running as a proxy of short-distance dispersal; death mimicry, immobility and anchoring were quantified but not considered in the analysis (see Table S1 in Appendix 3).

Statistical analyses

We fitted generalised linear mixed models with Bernoulli distribution in a Bayesian framework to investigate the presence/absence of each behaviour of interest separately. Each behaviour was binarised and analysed separately to account for the spiderlings lost during experiment. For aerial behaviours, that is, ballooning and rappelling, we considered the species and sampling date as predictors. We did a variable selection for the varying intercept and tried either nursery or site or both as varying intercepts.

For behaviours on water, that is, sailing, rowing, and running, we considered the species, wind and water speeds, weight of the spider, and sampling date as predictors. To control for a possible habituation to wind/water speed, we included the trial number as a co-variate in all models for waterborne behaviours. We used the spider ID as a varying intercept to account for repeated trials.

We used the default weakly informative priors of rstanarm (priors over parameters set as normal with a mean of 0.00 and a standard deviation of 2.5) and we fitted the models with four Markov chain Monte Carlo (MCMC) chains and 2000–4000 iterations and a warmup of 1000–2000 iterations. We used leave-one-out cross-validation values (LOO) to compare the predictive accuracy of fitted models and to select the most accurate model (Vehtari et al., 2017). We checked the models' convergence and stability visually and by making sure that Rhat values were not larger than 1.01 (Vehtari et al., 2020) and that effective sample sizes (ESS) were higher than 1000.

We represented the median of the posterior distribution and its uncertainty with a 95% credible interval. To help with interpretation, we used the probability of direction (pd), which is the probability that an effect goes in a particular direction, and the percentage of the distribution within the region of practical equivalence (ROPE) (Makowski, Ben-Shachar, Chen, et al., 2019; Makowski, Ben-Shachar, & Lüdtke, 2019). The thresholds beyond which the effect was considered as 'significant' (i.e. non negligible) were $pd > 95\%$ and $ROPE < 2.5\%$. All analyses were conducted with packages 'rstanarm' (Goodrich et al., 2020), 'modelbased' (Makowski et al., 2020) and 'bayestestR' (Makowski, Ben-Shachar, & Lüdtke, 2019) in R (R Core Team, 2020). The scripts used to generate the analyses are publicly available (see Data Accessibility Statement).

RESULTS

Propensity for airborne dispersal

For ballooning, the model with the lowest LOO value and therefore the highest predictive power included species and date of sampling with the nursery as varying intercept (Table 2; Table S2 in Appendix 3).

TABLE 2 Models with the best fit for each behaviour of interest to discriminate propensity for short-distance dispersal and propensity for long-distance dispersal

Dispersal	Response	Predictors
Airborne	Ballooning	Species + Date sample + (1 Nursery)
Airborne	Rappelling	Species + (1 Site) + (1 Nursery)
Waterborne	Sailing	Species + Wind water + Weight + Test + Date test + (1 ID)
Waterborne	Running	Species + Wind water + Test + (1 ID)
Waterborne	Rowing	Species + Wind water + Test + (1 ID)

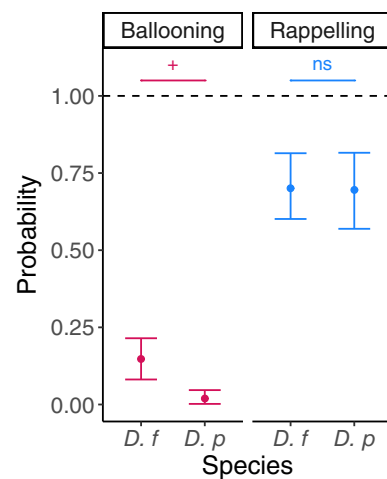


FIGURE 1 Probability of being ballooners (long-distance: red dots) and rappellers (short-distance: blue dots) estimated by the best-fitted model of each behaviour. Errorbars represent the 95% credible interval of the estimated probabilities. *D. f*, *Dolomedes fimbriatus*; *D. p*, *Dolomedes plantarius*

For rappelling, the best model was a null model with nursery and site ID as varying intercepts. Nonetheless, some models were equivalent according to LOO values and we present the results of the model including species as predictor, nursery and site ID as varying intercepts (Table 2; Table S2 in Appendix 3).

D. fimbriatus had a higher propensity to balloon than *D. plantarius* (Figure 1; estimated contrast = 2.16, credible interval = [0.35, 1.39]), $pd = 99.95\% > 95\%$, $ROPE = 0\% < 2.5\%$), but we did not find any difference in the propensity to rappel between species (Figure 1; $pd < 95\%$), nor an effect of sampling date on ballooning behaviour ($ROPE = 22.00\% > 2.5$).

Propensity for waterborne dispersal

For sailing, the model with the lowest LOO value included species, wind/water speed, spider weight, trial ID, date of test, and the interaction between species and weight as predictors, together with

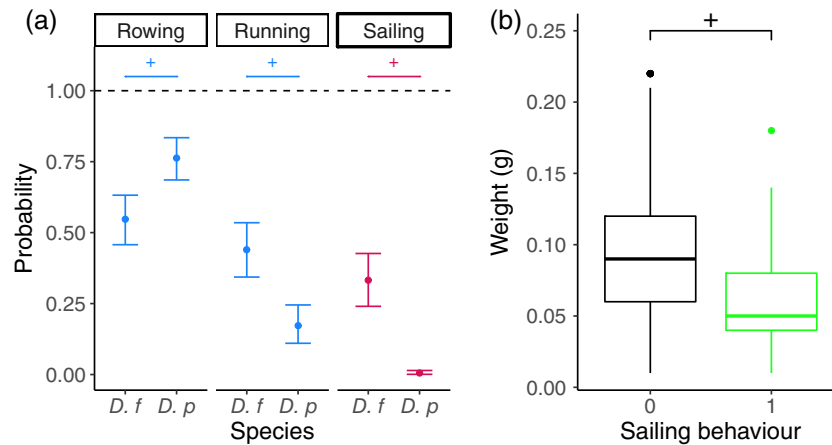


FIGURE 2 (a) Probability of showing rowing or running behaviours (short-distance: blue dots) or sailing behaviours (long-distance: red dots). (b) Influence of the weight on propensity to sail estimated by the best-fitted model of each behaviour (black: no sailing, green: sailing). Errorbars represent the 95% credible interval of the estimated probabilities. *D. f.*, *Dolomedes fimbriatus*; *D. p.*, *Dolomedes plantarius*

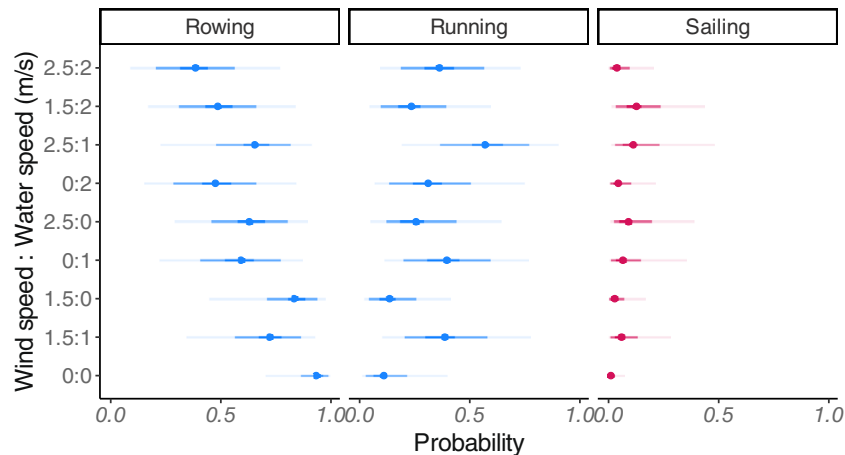


FIGURE 3 Estimated probability of showing sailing, rowing or running behaviours for different wind and water speeds, and for sailing, rowing and running models, respectively. The dot represents the estimated probability (median) and the light to dark line represents the 0, 0.5 and 0.95 credible intervals.

sampling date and the spider ID as varying intercepts (Table 2; Table S3 in Appendix 3). For both running and rowing behaviours, the best model included species and wind/water speeds, with trial and spider ID as varying intercepts (Table 2; Table S3 in Appendix 3).

We found a higher propensity to sail in *D. fimbriatus* than *D. plantarius* (estimated contrast = 4.43 [3.30, 5.68], $pd = 100\% > 95\%$, ROPE = 0% < 2.5%; see Figure 2a). Moreover, the propensity of sailing behaviour decreased with spiders' weight ($-0.74 [-1.26, -0.28]$, $pd > 95\%$, ROPE < 2.5%; Figure 2b), consequently heavier spiders sailed less than lighter ones. The presence of sailing behaviours was also influenced by wind and water speeds, with a convincingly lower propensity for sailing in absence of wind and water current ($pd > 95\%$, ROPE < 2.5%; Figure 3) except under 1.5:0 m/s wind: water speed condition, as well as less sailing behaviours under 1.5:2, 2.5:0 and 2.5:1 conditions ($pd > 95\%$, ROPE < 2.5%; Figure 3). We found the lowest propensity to sail during the first trial than during the second and third trials (Figure 4; $pd > 95\%$, ROPE < 2.5%),

whereas trials two and three likely did not differ (Figure 4; $pd < 95\%$). We did not find a significant effect of the date of sampling on the propensity to sail ($pd < 95\%$).

We found a higher propensity to run in *D. fimbriatus* than *D. plantarius* (estimated contrast = 1.33 [0.70, 1.94], $pd > 95\%$, ROPE < 2.5%; see Figure 2a). The propensity for running decreased between the first and second trials and between the second and third trials (Figure 4; $pd > 95\%$, ROPE < 2.5%). Moreover, the condition of 0:0 wind: water speed presented the lowest propensity for running, followed by conditions 1.5:0 and 2.5:0, which had the lowest number of runners ($pd > 95\%$, ROPE < 2.5%; Figure 3). Furthermore, we found higher propensity for running under condition 2.5:1 than under any other conditions (Figure 3).

We found a lower propensity to row in *D. fimbriatus* than in *D. plantarius* (estimated contrast = $-0.98 [-1.52, -0.44]$, $pd > 95\%$, ROPE < 2.5%; see Figure 2a). This behaviour was also used less frequently during the first trial than during the second and third trials

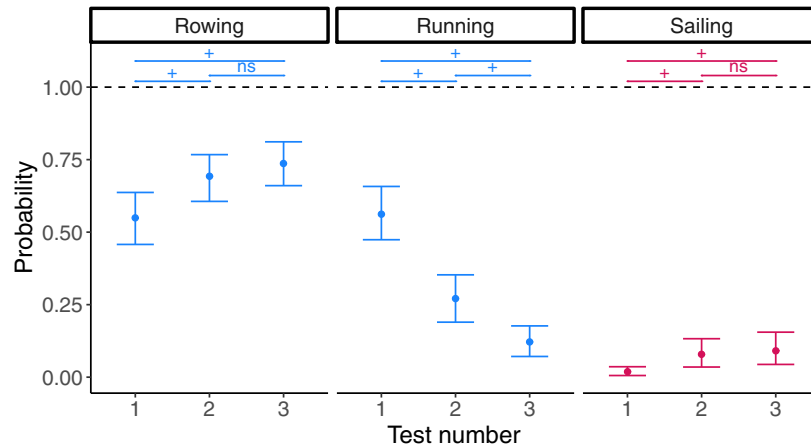


FIGURE 4 Probability of showing rowing or running behaviours (short-distance: blue dots), or sailing behaviours (long-distance: red dots) during the first, second or third experimental trial for each spider estimated by the best-fitting model for each behaviour. Errorbars represent the 95% credible interval of the estimated probabilities.

(Figure 4; $pd > 95\%$, $ROPE < 2.5\%$), whereas the trials two and three did not differ (Figure 4; $pd < 95\%$). Moreover, a higher propensity to row was found for the wind : water speed conditions 0:0, 1.5:0 and 1.5:1 than the other conditions ($pd > 95\%$, $ROPE < 2.5\%$; Figure 3).

DISCUSSION

As hypothesised, we observed that *D. fimbriatus* has higher propensity for long-distance dispersal than *D. plantarius*, both airborne and waterborne. We found a lower propensity to sail in heavier spiders when including spiders of both species. However, we could only partially validate the hypothesis that the frequency of waterborne movements was higher for *D. plantarius*. Indeed, it was true for the rowing behaviour, but we found a higher propensity to run in *D. fimbriatus*. Finally, we validated our hypothesis that the propensity to short-distance rappel did not differ between the two species.

Highest propensity for long-distance dispersal in *D. fimbriatus*

As expected, *D. fimbriatus* had a higher propensity for long-distance airborne dispersal than *D. plantarius*. This observation is in accordance with observations of specialist spiders having lower propensity to balloon than generalist spiders (Bonte, Vandenbroecke, et al., 2003). This is partly explained by the higher cost or the less likely it is for a habitat-specialist species to arrive in a suitable habitat. Hence, the propensity to disperse was higher in *D. fimbriatus*. Spiders that can balloon tend to have the ability to stand and to move on the water surface, that is, they have water-repellent legs (Hayashi et al., 2015). Accordingly, the same pattern was observed for waterborne spiders with higher sailing propensity for the more generalist spider. Moreover, the absence of this behaviour without wind and water current shows that the behaviour is wind-induced.

The high cost of airborne long-distance dispersal is well known (Bonte et al., 2012), e.g. spiders can land in an unsuitable habitat. Similar high cost was expressed in waterborne spiders with higher chance to unsuitable habitat for *D. plantarius* than *D. fimbriatus*. Indeed, spiders were less prone to sail during the first trial in a new, unknown environment than during the last two trials, which would indicate that this behaviour is potentially more controlled than ballooning. The effect of the spider body mass on the propensity for sailing is similar as for fishing spiders from North America (*Dolomedes triton*, see Suter, 1999), with smaller spiders having higher abilities to raise their body off the water and consequently to use sailing. Studying the propensity to sail for different stages might help to identify the age at which the fishing spiders are more prone to disperse on the water.

D. fimbriatus can occupy a wider variety of wet habitat while *D. plantarius* lives in site constantly wet, for example, along streams or on ponds (Dickel et al., 2022; Duffey, 2012; van Helsdingen, 1993). Because they have a higher propensity for sailing, the juveniles of *D. fimbriatus* could take better advantage from spring flooding more than those of *D. plantarius*, for long-distance dispersal. Lambeets, Hendrickx, et al. (2008) and Lambeets, Vandegehuchte, et al. (2008) found a similar pattern, with flooding facilitating the settlement of generalist spiders in a riverbank habitat. Specialist species like *D. plantarius* would preferably recolonise the previously occupied habitat after a flood (Lambeets, Vandegehuchte, et al., 2008). We suppose that during a flood, *D. plantarius* juveniles tend to hide more in the surrounding vegetation than *D. fimbriatus*, which could explain their different propensity for short-distance dispersal.

Contrasted propensity for short-distance dispersal

As hypothesised, we did not find difference in propensity for short-distance airborne (rappelling) dispersal between spiderlings of the two species. Contrary to ballooning, rappelling is influenced by the direct environment at small spatial scales, and not from inherited (genetically or not) information (Bonte et al., 2009). Our experimental setup where

the (context dependent) conditions were controlled and similar for both species might explain the absence of difference in propensity for rappelling.

We found two opposite patterns between species for short-distance waterborne dispersal behaviours. Individuals of *D. plantarius* used rowing more often than *D. fimbriatus*, and used running less often. Moreover, running propensity decreased between successive trials, whereas propensity to row increased. Even though the short-distance dispersal behaviours were called 'dispersal', these behaviours most probably characterise movements within rather than between populations. Our results would then be in line with observations from Lambeets and Bonte, 2009 and Lambeets, Van Ranst, and Bonte (2010) that generalist species do not use inherited information on water for their orientation and local movement in response to stress, as opposed to species specialised to water habitat.

Both behaviours might differ in their function, and running might be more related to immediate stress (Suter & Wildman, 1999), here in reaction to a new environment during the first trial. Since the running frequency was indeed the lowest in absence of wind and water current, wind and water current might represent stressful conditions. Running is for instance used by *D. triton* to escape predators (Hu & Bush, 2010; Suter et al., 1997). The difference in the propensity for rowing behaviour might be explained by the importance of flooding. Since *D. plantarius* lives in habitats with constant presence of water and is usually exposed to spring flooding, it could respond to flood more efficiently. On the other hand, *D. fimbriatus*, which is less frequently exposed to the water surface environment, could use only direct information from this unfamiliar environment. *D. fimbriatus* would then run away, behaviour not specific to the water environment.

Perspectives for future works on poorly documented behaviours

It would be interesting to estimate the abilities of species to settle in newly colonised sites. Here, we mainly focused on the first two phases of dispersal, that is, emigration and transfer, but the actual distance of dispersal (e.g. by sailing) remains largely unknown. Tracking spiderlings ballooning in the field is difficult, but a mark-recapture analysis could be used to track bigger juveniles on the water (e.g. adapting the method used on *D. triton* by Zimmermann & Spence, 1992). Regarding short-distance dispersal on water, it is difficult to differentiate between local-scale movements and actual dispersal behaviours. Rowing and running are sometimes used for short movement on the water, and to move back to the vegetation edge, or as an escape behaviour (Suter, 2013). Other behaviours like anchoring or death mimicry could be related to passive and uncontrolled short-distance dispersal. Nonetheless, anchoring is used for hunting or to rest on the surface (Gorb & Barth, 1994), and death mimicry is a stress-related behaviour, which we observed in less than 5% of the tests.

Consequences for conservation

New sites with *D. plantarius* were recently found in Europe (in Germany: Harms et al., 2009; in Spain: Bellvert et al., 2013; in Belarus: Ivanov et al., 2017; in Italy: Milano et al., 2018; in Norway: Fjellberg et al., 2018). Nonetheless, this apparent spread is most probably due to an increasing interest in protecting wetlands rather than an actual expansion of the species, as *D. plantarius* is most often observed when sampling for other species (e.g. see Bellvert et al., 2013). The seemingly growing interest for *D. plantarius* might also be related to its red-listed status (Baillie et al., 1996; Milano et al., 2021). In a related modelling study involving species distribution models, we found that *D. fimbriatus* might be a better candidate to spread northward than *D. plantarius* (Monsimet et al., 2020). This observation is in line with the fact that we did not find significant variation in the propensity for dispersal between species along the latitudinal gradient. A similar observation of the absence of latitudinal effect on propensity for dispersal was recently made in the wasp spider *Argiope bruennichi* (Wolz et al., 2020). Regardless, it would be interesting to evaluate the fecundity of these species, as Wolz et al. (2020) observed that the range expansion of *Argiope bruennichi* was (partly) driven by a higher reproductive investment in margin populations. Resolving the question of *Dolomedes* range expansion should guide decisions for the conservation of the species, especially for the red listed *D. plantarius*. Indeed, if the species does not expand, preserving the current populations is primordial as its Southern range will become unsuitable in the future (Leroy et al., 2013, 2014).

The presence of interconnected network of wetlands is highly necessary to conserve species (Gibbs, 1993), especially for spiders for which the management of hydrological functioning is fundamental (Lafage & Pétillon, 2016; Lambeets, Breyne, & Bonte, 2010; Lambeets, Vandegheuchte, et al., 2008). Moreover, the propensity of *D. fimbriatus* to use streams for long-distance dispersal might be limited by dams, and the conservation of this species could be considered in the management plan of dams, as done for fishes in Sweden (Lejon et al., 2009). Maintaining connectivity in the first 5 km around each presence site, which corresponds to the more frequent distance of airborne dispersal events (Thomas et al., 2003), is crucial to conserve current sites, promote expansion, and to conserve gene flow. For *D. plantarius*, this distance between populations should be even shorter, as two populations distant of less than a kilometre showed genetic differences in the United Kingdom (Vugdelić, 2006). It is also important to preserve the already existing habitats of *Dolomedes* because wetland restoration does not necessarily permit the relocation of species, even less so for specialist species (Hacala et al., 2020). Moreover, the higher propensity for long-distance dispersal of both waterborne and airborne spiders for *D. fimbriatus* compared to *D. plantarius* can have important consequences for persistence of the range in a changing climate.

Long-distance dispersal seems of primary importance for the sustainability and conservation of threatened species (Trakhtenbrot et al., 2005). Combining dispersal information, mark-recapture and

landscape genetic or genomic (reviewed by Manel et al., 2003; Manel & Holderegger, 2013) in models like the one developed by Allgayer et al. (2021) would permit to understand population dynamics of *Dolomedes* along streams. Ultimately, the gene flow and population dynamic might be threatened by habitat fragmentation and loss of interconnected wetlands due to limited propensity for long-distance dispersal, especially for *D. plantarius*.

AUTHOR CONTRIBUTIONS

Jérémy Monsimet, Julien Pétillon, Olivier Devineau, and Denis Lafage conceptualised the study. Jérémy Monsimet performed the experiments; Jérémy Monsimet, Nino Gardon and Léa Bataillard analysed the videos of the experiments. Jérémy Monsimet and Olivier Devineau implemented the statistical analyses. Denis Lafage provided laboratory resources. Jérémy Monsimet wrote the first draft of the paper, and all authors contributed substantially to revisions and content.

ACKNOWLEDGEMENTS

The authors thank Länsstyrelsen (Sweden) for allowing us to sample *Dolomedes* and all the landowners who gave access to their properties. The authors thank Lars Jonsson for giving us occurrences sites of both species in Sweden and for the help in sampling some spiders. The authors thank Gunnar Gunnarsson and Johan ElMBERG for giving us access to laboratory facilities at the University of Kristianstad (Sweden). The authors thank Karl Filipsson, Niclas Carlsson and Stina Eriksson for giving us access to the laboratory and aquariums at the University of Karlstad (Sweden).

CONFLICT OF INTEREST

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data and R scripts that support the findings of this study are openly available in Dataverse at <https://dataverse.no/dataset.xhtml?persistentId=doi:10.18710/2X6I2S>.

ORCID

Jérémy Monsimet  <https://orcid.org/0000-0001-9153-8401>

Julien Pétillon  <https://orcid.org/0000-0002-7611-5133>

Olivier Devineau  <https://orcid.org/0000-0002-7625-2816>

Denis Lafage  <https://orcid.org/0000-0002-6205-611X>

REFERENCES

- Allgayer, R.L., Scarpa, A., Fernandes, P.G., Wright, P.J., Lancaster, L., Bocedi, G. et al. (2021) Dispersal evolution in currents: spatial sorting promotes philopatry in upstream patches. *Ecography*, 44, 231–241.
- Baguette, M. & Van Dyck, H. (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecology*, 22, 1117–1129.
- Baillie, J., Gärdenfors, U., Groombridge, B., Rabb, G. & Stattersfield, A.J. (1996) *The IUCN red list of threatened species 1996*. Gland, Switzerland: IUCN.
- Bell, J.R., Bohan, D.A., Shaw, E.M. & Weyman, G.S. (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, 95, 69–114.
- Bellvert, A., Casals, A., Fonollosa, A., Dalmau, G. & Tobella, C. (2013) First record of *Dolomedes plantarius* (Clerck, 1758) (Araneae: Pisauridae) from the Iberian Peninsula. *Revista Ibérica de Aracnología*, 23, 109–111.
- Bonte, D., Clercq, N.D., Zwertvaegher, I. & Lens, L. (2009) Repeatability of dispersal behaviour in a common dwarf spider: evidence for different mechanisms behind short- and long-distance dispersal. *Ecological Entomology*, 34, 271–276.
- Bonte, D. & Lens, L. (2007) Heritability of spider ballooning motivation under different wind velocities. *Evolutionary Ecology Research*, 9, 817–827.
- Bonte, D., Lens, L., Maelfait, J.P., Hoffmann, M. & Kuijken, E. (2003) Patch quality and connectivity influence spatial dynamics in a dune wolfspider. *Oecologia*, 135, 227–233.
- Bonte, D., Lukáč, M. & Lens, L. (2008) Starvation affects pre-dispersal behaviour of Erigone spiders. *Basic and Applied Ecology*, 9, 308–315.
- Bonte, D., Travis, J.M., De Clercq, N., Zwertvaegher, I. & Lens, L. (2008) Thermal conditions during juvenile development affect adult dispersal in a spider. *Proceedings of the National Academy of Sciences*, 105, 17000–17005.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M. et al. (2012) Costs of dispersal. *Biological Reviews*, 87, 290–312.
- Bonte, D., Vandenbroecke, N., Lens, L. & Maelfait, J.P. (2003) Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proceedings of the Royal Society of London B: Biological Sciences*, 270, 1601–1607.
- Clobert, J., Galliard, J.-F.L., Cote, J., Meylan, S. & Massot, M. (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12, 197–209.
- Davidson, N.C. (2014) How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research*, 65, 934–941.
- De Meester, N. & Bonte, D. (2010) Information use and density-dependent emigration in an agrobiont spider. *Behavioral Ecology*, 21, 992–998.
- Dickel, L., Monsimet, J., Lafage, D. & Devineau, O. (2022) Characterization of habitat requirements of European fishing spiders. *PeerJ*, 10, e12806.
- Duffey, E. (2012) *Dolomedes plantarius* (Clerck, 1757) (Araneae: Pisauridae): a reassessment of its ecology and distribution in Europe, with comments on its history at Redgrave and Lopham Fen, England. *Bulletin of the British Arachnological Society*, 15, 285–292.
- Fjellberg, A., Løvbrekke, H. & Olsen, K.M. (2018) Additions and corrections to the Norwegian list of spiders (Araneae). *Norwegian Journal of Entomology*, 65, 13–21.
- Friard, O. & Gamba, M. (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7, 1325–1330.
- Frost, C.M., Graham, A.K. & Spence, J.R. (2013) Abiotic conditions rather than resource availability cues determine aerial dispersal behaviour in spiderlings of *Dolomedes triton* (Araneae: Pisauridae). *The Canadian Entomologist*, 145, 29–39.
- Gibbs, J.P. (1993) Importance of small wetlands for the persistence of local populations of wetland-associated animals. *Wetlands*, 13, 25–31.
- Goodacre, S.L., Martin, O.Y., Bonte, D., Hutchings, L., Woolley, C., Ibrahim, K. et al. (2009) Microbial modification of host long-distance dispersal capacity. *BMC Biology*, 7, 32.

- Goodrich, B., Gabry, J., Ali, I. & Brilleman, S. (2020) Rstanarm: Bayesian applied regression modeling via Stan. R package version 2.21.1 <https://mc-stan.org/rstanarm>
- Gorb, S.N. & Barth, F.G. (1994) Locomotor behavior during prey-capture of a fishing spider, *Dolomedes plantarius* (Araneae: Araneidae): galloping and stopping. *Journal of Arachnology*, 22, 89–93.
- Hacala, A., Le Roy, M., Sawtschuk, J. & Pétilion, J. (2020) Comparative responses of spiders and plants to maritime heathland restoration. *Biodiversity and Conservation*, 29, 229–249.
- Harms, D., Dunlop, J.A. & Schütt, K. (2009) Neue nachweise der gerandeten wasserspinn *Dolomedes plantarius* in Brandenburg (Araneae: Pisauridae). *Arachnologische Mitteilungen*, 7, 1–8.
- Hayashi, M., Bakkali, M., Hyde, A. & Goodacre, S.L. (2015) Sail or sink: novel behavioural adaptations on water in aerially dispersing species. *BMC Evolutionary Biology*, 15, 1–8.
- Hu, D.L. & Bush, J.W.M. (2010) The hydrodynamics of water-walking arthropods. *Journal of Fluid Mechanics*, 644, 5–33.
- Ivanov, V., Prishchepchik, O. & Setrakova, E. (2017) *Dolomedes plantarius* (Araneae, Pisauridae) in Belarus: records, distribution and implications for conservation. *Arachnologische Mitteilungen*, 54, 33–37.
- Lafage, D. & Pétilion, J. (2016) Relative importance of management and natural flooding on spider, carabid and plant assemblages in extensively used grasslands along the Loire. *Basic and Applied Ecology*, 17, 535–545.
- Lambeets, K. & Bonte, D. (2009) Between-population variation in home-ward orientation behaviour in two riparian wolf spiders. *Behavioural Processes*, 82, 62–66.
- Lambeets, K., Breyne, P. & Bonte, D. (2010) Spatial genetic variation of a riparian wolf spider *Pardosa agricola* (Thorell, 1856) on lowland river banks: the importance of functional connectivity in linear spatial systems. *Biological Conservation*, 143, 660–668.
- Lambeets, K., Hendrickx, F., Vanacker, S., Van Looy, K., Maelfait, J.P. & Bonte, D. (2008) Assemblage structure and conservation value of spiders and carabid beetles from restored lowland river banks. *Biodiversity and Conservation*, 17, 3133–3148.
- Lambeets, K., Van Ranst, J. & Bonte, D. (2010) Is movement behavior of riparian wolf spiders guided by external or internal information? *Journal of Arachnology*, 38, 313–318.
- Lambeets, K., Vandegheuchte, M.L., Maelfait, J.P. & Bonte, D. (2008) Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *Journal of Animal Ecology*, 77, 1162–1174.
- Lejon, A.G.C., Renöfält, B.M. & Nilsson, C. (2009) Conflicts associated with dam removal in Sweden. *Ecology and Society*, 14, 24.
- Leroy, B., Bellard, C., Dubos, N., Colliot, A., Vasseur, M., Courtial, C. et al. (2014) Forecasted climate and land use changes, and protected areas: the contrasting case of spiders. *Diversity and Distributions*, 20, 686–697.
- Leroy, B., Paschetta, M., Canard, A., Bakkenes, M., Isaia, M. & Ysnel, F. (2013) First assessment of effects of global change on threatened spiders: potential impacts on *Dolomedes plantarius* (Clerck) and its conservation plans. *Biological Conservation*, 161, 155–163.
- Makowski, D., Ben-Shachar, M. & Lüdecke, D. (2019) bayestestR: describing effects and their uncertainty, existence and significance within the Bayesian framework. *Journal of Open Source Software*, 4, 1541.
- Makowski, D., Ben-Shachar, M.S., Chen, S.H.A. & Lüdecke, D. (2019) Indices of effect existence and significance in the Bayesian framework. *Frontiers in Psychology*, 10, 2767.
- Makowski, D., Lüdecke, D. & Ben-Shachar, M. S. (2020) Modelbased: estimation of model-based predictions, contrasts and means. CRAN <https://github.com/easystats/modelbased>
- Manel, S. & Holderegger, R. (2013) Ten years of landscape genetics. *Trends in Ecology & Evolution*, 28, 614–621.
- Manel, S., Schwartz, M.K., Luikart, G. & Taberlet, P. (2003) Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution*, 18, 189–197.
- Milano, F., Blick, T., Cardoso, P., Chatzaki, M., Fukushima, C.S., Gajdoš, P. et al. (2021) Spider conservation in Europe: a review. *Biological Conservation*, 256, 109020.
- Milano, F., Pantini, P., Cavalcante, R. & Isaia, M. (2018) Notes on the Italian distribution of *Dolomedes plantarius* (Clerck, 1757), species assessed for the IUCN red list (Araneae: Pisauridae). *Fragmenta Entomologica*, 50, 69–74.
- Monsimet, J., Devineau, O., Pétilion, J. & Lafage, D. (2020) Explicit integration of dispersal-related metrics improves predictions of SDM in predatory arthropods. *Scientific Reports*, 10, 1–12.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Pétilion, J., Deruytter, D., Decae, A., Renault, D. & Bonte, D. (2012) Habitat use, but not dispersal limitation, as the mechanism behind the aggregated population structure of the mygalomorph species *Atypus affinis*. *Animal Biology*, 62, 181–192.
- R Core Team. (2020) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Radchuk, V., Reed, T., Teplitsky, C., van de Pol, M., Charmantier, A., Hassall, C. et al. (2019) Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications*, 10, 1–14.
- Ronce, O. (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, 38, 231–253.
- Sturm, M., Racine, C. & Tape, K. (2001) Climate change: increasing shrub abundance in the Arctic. *Nature*, 411, 546–547.
- Suter, R.B. (1999) Cheap transport for fishing spiders (Araneae, Pisauridae): the physics of sailing on the water surface. *Journal of Arachnology*, 27, 489–496.
- Suter, R.B. (2013) Spider locomotion on the water surface: biomechanics and diversity. *Journal of Arachnology*, 41, 93–101.
- Suter, R.B. & Gruenwald, J. (2000) Predator avoidance on the water surface? Kinematics and efficacy of vertical jumping by *Dolomedes* (Araneae, Pisauridae). *Journal of Arachnology*, 28, 201–210.
- Suter, R.B., Rosenberg, O., Loeb, S., Wildman, H. & Long, J. (1997) Locomotion on the water surface: propulsive mechanisms of the fisher spider. *Journal of Experimental Biology*, 200, 2523–2538.
- Suter, R.B. & Wildman, H. (1999) Locomotion on the water surface: hydrodynamic constraints on rowing velocity require a gait change. *Journal of Experimental Biology*, 202, 2771–2785.
- Thomas, C.F.G., Brain, P. & Jepson, P.C. (2003) Aerial activity of linyphiid spiders: modelling dispersal distances from meteorology and behaviour. *Journal of Applied Ecology*, 40, 912–927.
- Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, 11, 173–181.
- Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D. et al. (2013) Dispersal and species' responses to climate change. *Oikos*, 122, 1532–1540.
- Trochet, A., Courtois, E.A., Stevens, V.M., Baguette, M., Chaine, A., Schmeller, D.S. et al. (2016) Evolution of sex-biased dispersal. *The Quarterly Review of Biology*, 91, 297–320.
- Van Dyck, H. & Baguette, M. (2005) Dispersal behaviour in fragmented landscapes: routine or special movements? *Basic and Applied Ecology*, 6, 535–545.
- van Hedsdingen, P.J. (1993) Ecology and distribution of *Dolomedes* in Europe (Araneida: Dolomedidae). *Bolletino Dell'Accademia Gioenia Di Scienze Naturali*, 26, 181–187.
- Vehtari, A., Gelman, A. & Gabry, J. (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27, 1413–1432.
- Vehtari, A., Gelman, A., Simpson, D., Carpenter, B. & Bürkner, P.-C. (2020) Rank-normalization, folding, and localization: an improved R-hat for assessing convergence of mcmc. *Bayesian Analysis*, 1, 1–28.

- Vugdelić, M. (2006) *Genetic relations within and among Dolomedes aquatic spiders*. PhD Thesis. Norwich: University of East Anglia.
- Wolz, M., Klockmann, M., Schmitz, T., Pekár, S., Bonte, D. & Uhl, G. (2020) Dispersal and life-history traits in a spider with rapid range expansion. *Movement Ecology*, 8, 1–11.
- Woolley, C., Thomas, C.F.G., Hutchings, L., Goodacre, S., Hewitt, G.M. & Brooks, S.P. (2007) A novel trap to capture ballooning spiders. *Journal of Arachnology*, 35, 307–312.
- World Spider Catalog (2022). World spider catalog. Version 23.0. *Natural History Museum Bern*. <http://wsc.nmbe.ch> [Accessed 14th February 2022].
- Zimmermann, M. & Spence, J.R. (1992) Adult population dynamics and reproductive effort of the fishing spider *Dolomedes triton* (Araneae, Pisauridae) in central Alberta. *Canadian Journal of Zoology*, 70, 2224–2233.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1 Supporting Information

How to cite this article: Monsimet, J., Pétilion, J., Devineau, O., Gardoni, N., Bataillard, L. & Lafage, D. (2022) Contrasted propensity for waterborne and airborne dispersal between two closely related semi-aquatic spider species. *Insect Conservation and Diversity*, 1–10. Available from: <https://doi.org/10.1111/icad.12596>