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1 **Influence of individual density and habitat availability on long-distance dispersal in a**
2 **salt-marsh spider.**

3 Running head: Dispersal differs among stages in a salt-marsh spider.

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5

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15 Dispersal is a key process in metapopulation dynamics and metacommunity assembly
16 as it may be affected by a variety of factors acting at different spatial scales. While dispersal
17 is known to evolve in response to landscape-related selection pressures, local dynamics are
18 merely driven by conditional responses, for instance by habitat quality and density. Local and
19 regional factors are thus expected to impact dispersal, either synergistically or
20 antagonistically. Moreover, such responses do not need to coincide among all life stages
21 because different life stages are expected to incur different costs, either intrinsically due to for
22 instance differences in size or extrinsically because of demographic changes. Our general
23 objective is consequently to test for the likely opposite effects of main factors acting on
24 dispersal, i.e. local density and habitat configuration, at different life-stages in a salt marsh
25 inhabiting spider *Pardosa purbeckensis* (FOP. Cambridge 1895). Using a combination of both
26 field and laboratory experiments on pre-dispersal behaviour, we demonstrate a significant
27 negative density-dependence for natal dispersal, but no alike effect at the adult stage. No
28 effects of the local habitat structure were detected. Therefore, good mother body condition
29 could be interpreted by juveniles during the phase of maternal care as suitable living
30 conditions, decreasing emigration rate. Although dispersal is known to have a genetic basis,
31 local factors eventually overrule this source of variation.

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33 KEY WORDS: *Pardosa purbeckensis*, ballooning, habitat fragmentation, kin density-
34 dependence.

INTRODUCTION

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Dispersal is seen as movements of individuals, either natal or breeding dispersal, that could impact gene flow across space (Ronce, 2007). It is then an adaptive process to escape from local habitat deterioration or as bet-hedging strategy (Clobert et al. 2012; Matthysen 2012; Duputié & Massol 2013), taking away the animal, or plant, from its original territory (Southwood 1962) and modifying meta-population structure and species distribution. Thus, in a context of rapid global change, dispersal is considered as a key process in metapopulation dynamics and metacommunity assembly. Emigration may then allow individuals to find better living conditions, higher mating success and leads to genetic exchanges (Bowler & Benton 2005). Although risks endured during or after dispersal can be costly, whether from a metabolic point of view, a time during which individuals are not feeding or mating, with predation risks or either a risk to arrive in a less suitable patch (Duputié & Massol 2013), especially when suitable patches are isolated with a high mortality risk in the matrix (Bonte et al. 2012), this behaviour can be yet selected when emigration becomes more advantageous for fitness than remaining in the native patch (Bowler & Benton 2005). In most theoretical studies, dispersal is seen as a genetically, and unconditional, fixed strategy, however, phenotype-dependent (individual state) and condition-dependent (external information) dispersal (Clobert et al. 2009) are the most likely strategies supported by empirical literature (Bowler & Benton 2005; Bonte & de la Peña 2009).

The competition for resources due to high densities might be one of the main conditional factors causing emigration (Denno & Peterson 1995; Bowler & Benton 2005). Individuals might perceive an increase of density, and thus start emigration before reaching the carrying capacity of the population's environment. However, densities differ among the different life stages of a population; mortality at a given stage can indeed increase density in

1 another one (Schröder et al. 2014). The intensity of competition will thus vary among these
2 stages, and higher dispersal rate will be expected in stages where the competition is the
3 strongest and costs lowest (e.g. during the development phase; Bonte et al. 2012). For
4 instance, competition in spiders might be strongest at the juvenile stage than at the adult stage
5 as most juveniles die before adult stage, mainly because of cannibalism, among juveniles or
6 adults upon juveniles (Wise 2006). Avoidance of kin competition and inbreeding should also
7 increase dispersal rates on early stages (Gandon 1999), kin density could be expected to also
8 play a role in dispersal. This kin density can be used actually, according to the public
9 information principle, as an estimator of the reproductive success of conspecifics, and thus of
10 habitat quality (Doligez et al. 2002). In the same manner, juveniles can also indirectly
11 estimate habitat quality through their mother body condition during the phase of maternal care
12 (Mestre & Bonte 2012). Dispersal density-dependence has been tested for several taxa (both
13 invertebrates and vertebrates; review in Bowler & Benton 2005). Given all these causes, most
14 studies found positive effects of density dependence on long-distance dispersal, either for
15 insects or for vertebrates (Denno & Peterson 1995; Bowler & Benton 2005). Positive effects
16 of density were also demonstrated in spiders for both short- and long-distance dispersal
17 (rapelling is sex-ratio dependent and ballooning is increased by the presence of silk threads;
18 De Meester & Bonte 2010).

19 Dispersal is known to be a central trait in life history (Bonte & Dahiriel 2017) and to
20 some degree under genetic control (Saastamoinen 2018). We lack, however insights whether
21 factors related to local conditions eventually overrule this genetic signal in an adaptive way
22 (Bonte & Dahiriel 2017), so whether there is a hierarchy in the eventual drivers of dispersal
23 (Legrand et al. 2015). Habitat configuration, and in particular local habitat conditions, as well
24 as landscape suitability, are known to impose metapopulation-level selection, thereby leading
25 to evolutionary divergence in dispersal across landscapes. Habitat availability and risks of

1 moving to an unsuitable matrix will affect costs, so large costs will select against dispersal
2 (Travis & Dytham 1999; Heino & Hanski 2001; Poethke & Hovestadt 2002). Then if habitat
3 is scarce, local adaptation in dispersal can occur (Bonte et al. 2010). This highlights the
4 importance of multifactorial approaches (Matthysen 2012), although seldom explored (but see
5 Legrand et al. 2015). Most studies focused on dispersal assess at meta-population level, but
6 within population variation in dispersal might exist. Such polymorphism is especially
7 expected when matrix effect are strong (Bonte et al. 2010).

8 Salt marshes are ideal systems to study within population dispersal as they present a
9 highly habitat fragmentation mainly due to human activities leading to a great spatial
10 heterogeneity (Valéry et al. 2004) and a very high primary production, supporting abundant,
11 yet poorly-diversified, prey items (mainly the amphipod *Orchestia gamarella* (Pallas 1766);
12 Laffaille et al. 2005). At soil surface, dominant salt-marsh predators are usually wolf spiders
13 (Döbel et al. 1990; Pétilion et al. 2005), for which *Orchestia gamarella* might be the main
14 prey of adults (Foucreau et al. 2012). Several species of this family are known to express
15 long-distance dispersal, mainly at early stages of development. Lycosids express the
16 stereotype pre-dispersal “tip-toe” behaviour at the top of vegetation to receive the wind
17 necessary for ballooning (Richter 1970; Bonte & Lens 2007). The salt-marsh specialist
18 species *Pardosa purbeckensis* (FOP. Cambridge 1895) is known to balloon (the main mode of
19 long-distance dispersal for spiders, as for some other invertebrates) mainly on its early stage
20 of development (second-instar: i.e. two-three weeks) but also during the adult phase although
21 at lower rates. This species expresses the stereotype pre-dispersal “tip-toe” behaviour at the
22 top of vegetation to receive the wind necessary for ballooning (Richter 1970; Bonte & Lens
23 2007). This pre-dispersal behaviour as already been studied on various spider species both on
24 the field, by the use of different kind of traps (e.g. Duffey 1956; Woolley et al. 2007) and on
25 laboratory conditions (e.g. Richter 1970; Weyman 1995; De Meester & Bonte 2010).

1 availability and a patch with a diameter larger than 200 m will be considered to provide high
2 habitat availability.

3

4 *Juvenile dispersal under laboratory conditions*

5 In order to test whether density and maternal habitat availability influence juveniles'
6 propensity to balloon, ten females with cocoon of *P. purbeckensis* were hand-collected in
7 each patches (3 sizes * 6 replicates = 18 patches) the 13th and 14th of June 2014 during the
8 peak of reproduction, when females are the most susceptible to carry a cocoon.

9 The experiment was then conducted in laboratory conditions from the 16th of June to
10 the 15th of July 2014 (until no dispersal attempt was observed). Temperature was regulated at
11 $25 \pm 2^\circ\text{C}$, photoperiod was 16/8 hr day/night regime from 6 am to 10 pm.

12 Each female was then placed with its cocoon randomly in a “smooth flower pot” of 11
13 cm diameter and 10 cm high, filled with two centimetres height of sand and one sticky trap of
14 35 cm high (consisting in a wood stick with a band of double face tape just upper the top of
15 pot; Duffey, 1956) was installed in the middle of the pot. A sticky tape was placed at the top
16 of the pot to check for possible escaping. Once juveniles hatched (thus they had no direct
17 experience with their natal environment) and left their mother’s abdomen, the female was
18 removed from the pot to avoid predation.

19 Just after hatching, Females were weighted to get a proxy of the number of eggs. The
20 number of juveniles in each cocoon, and thus by “pot”, was estimated using the equation $y =$
21 $3.8057x + 25.049$, with x as the female mass (derived from Puzin et al. 2011).

22 Artificial wind, between 0.2 to 2.5 m/s, was obtained thanks to ventilators; as these
23 velocities are the most adequate for spiders to engage dispersal (nonetheless, less dispersal is

1 observed when it is faster than 1.2 m/s). These ventilators were running during three hours
2 every two days (adapted from Bonte et al. 2007). During these three hours, sticky traps were
3 continuously checked and climbing juveniles removed, counted and kept in ethanol 70; sticky
4 traps were thus effective again for subsequent experiments. The location of pots was changed
5 before each session.

6

7 *Adult dispersal on the field*

8 To assess whether the density and habitat availability influence the dispersal
9 propensity of adults, we sampled individuals in each patche (3 sizes * 6 replicates = 18
10 patches), all dominated by the plant *Atriplex portulacoides* L., 1753.

11 In each patch, eight sticky traps of 70 cm high (with the double face tape placed just
12 upper the top of surrounding vegetation) were placed by pairs at one meter of a pitfall trap
13 (i.e. four pitfall traps per patch, 144 sticky traps in total). Sticky traps were weekly checked
14 and climbing adults removed, counted and kept in ethanol 70; sticky traps were thus effective
15 during all sampling sessions. Pitfall traps (polypropylene cups of 10 cm diameter, 17 cm
16 deep) were placed at 10 m from each other (to avoid interference between them) and filled of
17 ethylene-glycol. Traps were visited weekly from April 27th to June 15th of 2012, during the
18 main period of adults' activity, except during one week, where the salt-marsh was inundated
19 by a high tide. We could test for the effect of local density on dispersal by pair-matching
20 sticky traps with pitfall traps.

21

22 *Data analyses*

1 In order to assess differences in the proportion of dispersers according to density and
2 gradient of habitat availability, binomial Generalized Linear Models (logit link) were perform
3 for both juveniles and adults.

4 1) The proportion of juvenile dispersers (i.e. the ratio of the number of juveniles
5 caught by sticky traps / the estimated number of juveniles) was used as dependent variable,
6 the gradient of habitat availability as explanatory variable and the estimated number of
7 juveniles as a covariate.

8 2) The proportion of adult dispersers (i.e. the ratio of the number of adults caught by
9 sticky traps / the number of adults caught by pitfall traps) was used as dependent variable, the
10 gradient of habitat availability as fixed factor and the activity-density (i.e. the number of
11 adults caught by pitfall traps) as a covariate.

12 If the covariate-by-factor interaction was not significant (homogeneity of slopes in
13 model 1), a second binomial GLM (model 2) was used to test effects of factor and covariate
14 independently. Post-hoc Tukey tests, with Bonferroni correction, were performed in case of
15 significant effect of habitat availability.

16 All data analyses were performed using R software packages (R Development Core
17 Team 2014).

18

19

RESULTS

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Juvenile dispersal under laboratory conditions

1 The estimated number of juveniles had a significant negative effect on the proportion
2 of juvenile dispersers of *P. purbeckensis* (Table 1, Fig. 1). The gradient of habitat availability
3 had no effect on dispersal.

4 As interaction between covariate and factor was nearly significant ($p = 0.060$), we
5 tested separately the effect of density for each modality of habitat availability. In each
6 modality, the estimated number of juveniles had a significant negative effect on the
7 proportion of juvenile dispersers (LR $\chi^2 = 34.17$, $p < 0.001$; LR $\chi^2 = 10.47$, $p = 0.001$; LR $\chi^2 =$
8 3.91 , $p = 0.048$, in low, medium and high habitat availability respectively).

9

10 *Adult dispersal on the field*

11 During the experiment, only adults of *P. purbeckensis* (both males and females) were
12 caught on sticky traps. Neither the local activity-density, nor the gradient of habitat
13 availability had an effect on the proportion of dispersers (Table 2).

14

15 DISCUSSION

16 *Density dependence*

17 We found a significant effect of density only for juveniles of *P. purbeckensis* in the
18 lab' experiment, where density could represent here kin competition. The proportion of
19 juvenile dispersers was negatively correlated to the estimated number of juveniles. At first,
20 this negative density-dependence can be surprising because individuals experiencing high
21 densities should be submitted to more competition for resources and be more likely to
22 disperse (Denno & Peterson 1995; Travis et al. 1999; Bowler & Benton 2005). Several

1 hypotheses could explain such a result, as foraging facilitation (Kuussaari et al. 1996; Roland
2 et al. 2000) or use of public information during the phase of maternal care. In this latter case,
3 juveniles experiencing high densities can interpret this as a proxy of better living conditions
4 (Stamps 1988; Baguette et al. 2011) (whereas in case of positive density-dependence, density
5 would be perceived as a proxy for competition intensity). This has been shown in a study on
6 the collared flycatcher *Ficedula albicollis* (Temminck 1815), with higher dispersal rates when
7 offspring quantity or quality decrease (Doligez et al. 2002). Given the fact that juvenile
8 cannibalism is strong in lycosid spiders (Vanden Borre et al. 2006; Wise 2006), high densities
9 are not expected to be related to individual fitness benefits. Instead, and as shown in the
10 spider *Erigone dentipalpis* (Wider 1834) (Mestre & Bonte 2012), such a pattern can be more
11 likely attributed to anticipatory maternal effects. Since maternal size and clutch size in
12 *Pardosa* species are positively related to habitat quality, juvenile densities after hatching
13 (when all hitchhike the female; Bonte et al. 2006) can provide direct information on the
14 habitat quality while they do not have yet the ability to explore the habitat (Massot et al.
15 2002). Such a strategy has been shown to be extremely relevant when environmental
16 conditions are spatiotemporally correlated, as can be expected in high productive salt marsh
17 systems (Burgess & Marshall 2014).

18 As expected, no density-dependence was found for the adult stage of *P. purbeckensis*.
19 Densities of adults are actually expected to be lower than that of juveniles, which decreases
20 competition, and thus dispersal motivation of adults. As an example, cannibalism is highly
21 widespread in juveniles of *Pardosa*, including the days after hatching (e.g. *P. lugubris*; Edgar
22 1971, *P. amentata*; Hvam et al. 2005). Edgar (1971) found that 85% of juveniles of the close
23 species *Pardosa lugubris* (Walckenaer 1802) die before the first winter due to cannibalism
24 and intraguild predation, resulting in low densities of adults, with still a high mortality rate
25 during that stage. But then, this behaviour can play an important role in this type of lab

1 experiment, as it could interfere with total number of dispersers (whether by decreasing the
2 number of individuals that could disperse because of deaths, or by increasing dispersal to flee
3 cannibals). More-over, while smaller prey items can be limited for juveniles, large prey items
4 *Orchestia gamarella*, do not appear to be limiting at all (Pétillon et al. 2009).

5

6 *Effect of habitat availability*

7 The gradient of habitat availability did not influence the proportion of dispersers
8 (neither juveniles, nor adults). This conflicts with our expectation of less dispersal with low
9 degree of habitat availability (Travis & Dytham 1999). Indeed, small patches are more likely
10 to be isolated, and the risk of moving in an unsuitable site is higher. Then selection will
11 favour low dispersal rates. On the other hand, a negative correlation between patch size and
12 emigration rate has been found in several studies on other long-dispersal species (e.g. for
13 butterflies: Hill et al. 1996; Kuussaari et al. 1996; Baguette et al. 2000; beetles: Kareiva 1985;
14 or bush cricket: Kindvall 1999), either because of an edge effect, with more chance to
15 encounter the edge on small patches (Stamps et al. 1987) or due to demographic effects
16 (Andreassen & Ims 2001). These species perform active dispersal, i.e. they can choose where
17 they can settle, whereas spiders, although they control the emigration decision, are completely
18 dependent to spatial configuration and wind currents and cannot choose their immigration site
19 (Bell et al. 2005). Then dispersal risks and costs of spiders, or other passive dispersers, might
20 be different than for active dispersers, which could explain different strategies. As we found
21 no difference in dispersal rate according to the gradient of habitat availability, either other
22 factors might be involved in demographic dynamics and act at a local scale rather than at the
23 patch scale, or there is no genetic differentiation and thus no local adaptation at this scale.

24

CONCLUSION

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In conclusion, when studying dispersal polyphormism in a spider metapopulation (which has been few studied, although expected at that scale; Bonte et al. 2010), we document for the first time a negative density-dependence in juveniles suggesting conditional dispersal driven by maternal effect (as indicator on habitat quality) rather than by genetically based factors (habitat structure of mother).

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1 **Tables**

2 Table 1.

3 GLM (Binomial distribution) of the proportion of juvenile dispersers of *P. purbeckensis*
4 according to estimated number of juveniles and the gradient of habitat availability
5 (significance: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). LR χ^2 and p are given for model 2 as
6 the interaction between factors was not significant.

Variable	Factor	LR χ^2	df	P
Proportion of juvenile dispersers	Estimated N juveniles	40.20	1	< 0.001 ***
	Habitat availability	4.13	2	0.127

7

8

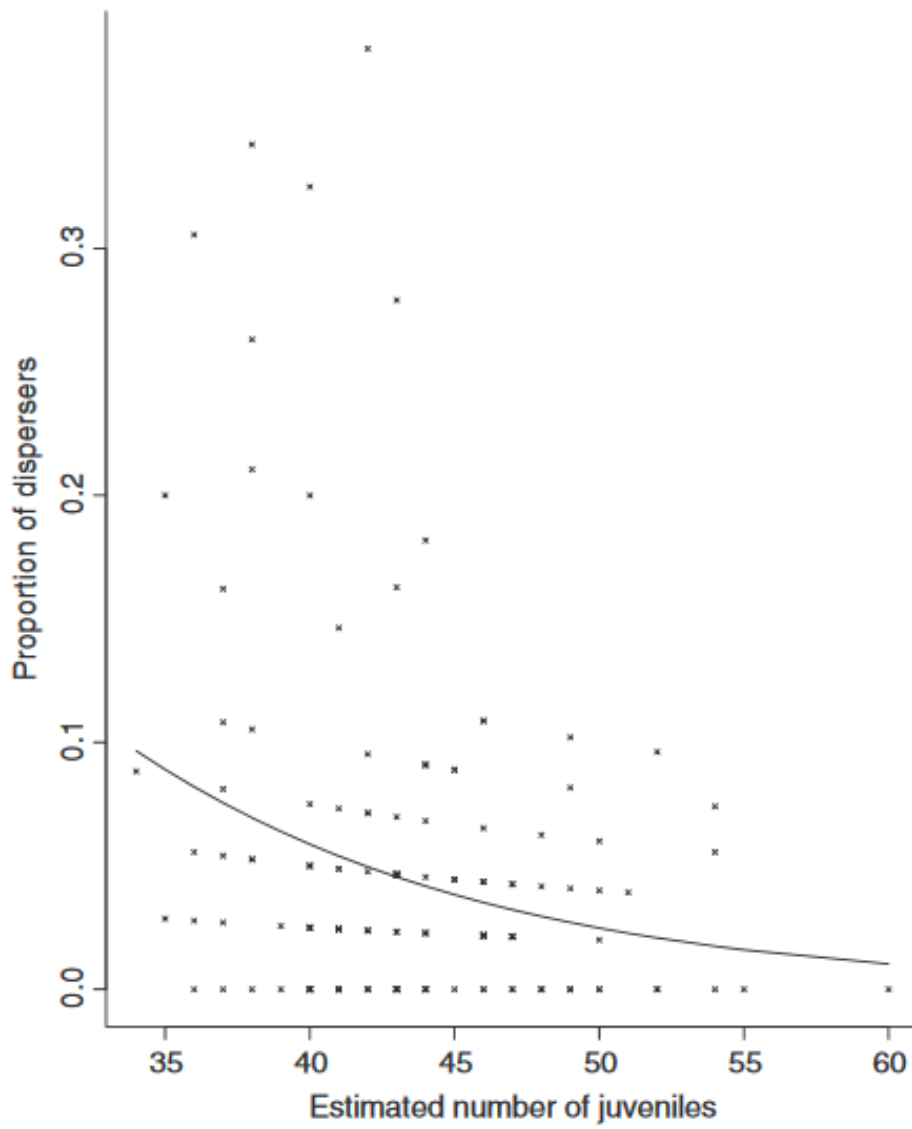
9 Table 2.

10 GLM (Binomial distribution) of the proportion of adult dispersers according to the activity-
11 density and the gradient of habitat availability (significance: *: $P < 0.05$; **: $P < 0.01$; ***: P
12 < 0.001). LR χ^2 and p are given for model 2 as the interaction between factors was not
13 significant.

Variable	Factor	LR χ^2	df	P
Proportion of adult dispersers	Activity density	0.12	1	0.734
	Habitat availability	4.58	2	0.102

14

1 **Figure caption**



2

3 Fig. 1. - Density-dependence of dispersal of *P. purbeckensis*' juveniles.