LETTER

The importance of growing up: juvenile environment influences dispersal of individuals and their neighbours

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Abstract

Dispersal is a key ecological process that is strongly influenced by both phenotype and environment. Here, we show that juvenile environment influences dispersal not only by shaping individual phenotypes, but also by changing the phenotypes of neighbouring conspecifics, which influence how individuals disperse. We used a model system (*Tribolium castaneum*, red flour beetles) to test how the past environment of dispersing individuals and their neighbours influences how they disperse in their current environment. We found that individuals dispersed especially far when exposed to a poor environment as adults if their phenotype, or even one-third of their neighbours' phenotypes, were shaped by a poor environment as juveniles. Juvenile environment therefore shapes dispersal both directly, by influencing phenotype, as well as indirectly, by influencing the external social environment. Thus, the juvenile environment of even a minority of individuals in a group can influence the dispersal of the entire group.

Keywords

informed dispersal, condition dependence, phenotype dependence, juvenile environment, *Tribolium castaneum*, red flour beetles, density-dependent dispersal, colonisation, neighbours, social environment.

Ecology Letters (2019) **22**: 45–55

INTRODUCTION

Dispersal is a key ecological process that can increase fitness by allowing individuals to respond to environmental variation (Ronce 2007; Clobert *et al.* 2012; Matthysen 2012). For example, individuals that disperse may escape from harsh or competitive environments or may be more likely to find mates (Gandon 1999; Palmqvist *et al.* 2000; Leturque & Rousset 2002; Perez-Gonzalez & Carranza 2009). However, dispersal is also risky. Mortality during dispersal can be high, and there is no guarantee the habitat into which individuals arrive will be more favourable than the habitat they left behind (Bonte *et al.* 2012; Travis *et al.* 2012). How then do individuals decide to disperse when both leaving and staying in their current habitat carry risk? This remains a central question within evolutionary ecology (Cote *et al.* 2010; Bonte *et al.* 2012; McConkey *et al.* 2012; Travis *et al.* 2013; Green *et al.* 2015; Heino *et al.* 2015), especially as individual dispersal decisions have lasting consequences for the evolution, persistence and spread of populations and species (Fisher 1937; Skellam 1951; Levin *et al.* 2003; Kokko & López-Sepulcre 2006; Jongejans *et al.* 2008; Baguette *et al.* 2013; Kubisch *et al.* 2014; Canestrelli *et al.* 2016; Bonte & Dahirel 2017).

One way that individuals evaluate the benefits of dispersal relative to the risks is by acquiring information from their surroundings (Valone 1989; Danchin *et al.* 2004; Clobert *et al.*

2009; Poethke *et al.* 2011; Clutton-Brock & Lukas 2012). For example, the odour of urine can trigger dispersal decisions in mice by communicating information about social environment, such as the relatedness, competitiveness or mating status of neighbouring conspecifics (Isles *et al.* 2002; Latham & Mason 2004). Whether mice ignore this information or use it to decide whether or not to disperse depends on their age, sex and social status (Latham & Mason 2004). Thus, dispersal is driven both by organisms' internal physiological and behavioural states (called *phenotype dependence*) as well as by the information that organisms gather about their external surroundings at the time of dispersal (called *condition dependence*, where condition refers to an individual's external surroundings, not its phenotype, Clobert *et al.* 2009).

The environment experienced as a juvenile (hereafter: *juvenile environment*) can strongly mediate interactions between phenotype dependence and condition dependence. Early development can influence phenotype dependence by changing an individual's dispersal capacity or its dispersal behaviour (Clobert *et al.* 2009). For example, developing at high density increases dispersal capacity of the planthoppers *Prokelisia marginata* (van Duzee) and *Prokelisia dolus* (Wilson) by triggering production of fully-winged migratory morphs (Denno & Roderick 1992). Early environment also influences dispersal behaviour, such as of the western black widow spider (*Latrodectus hesperus* Chamberlin & Ivie), which disperses less

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via ballooning behaviour when reared in isolation in the laboratory than when reared in cohorts under more natural conditions (Johnson *et al.* 2015). Studies such as these have been tremendously informative in revealing factors that alter patterns of dispersal within natural habitats. However, the degree to which individuals disperse as a result of their current environment vs. as a result of how their phenotype was shaped by their juvenile environment remains less well understood. Manipulative experiments that separate development from dispersal are necessary to disentangle these two processes.

Juvenile environment affects dispersal not only by directly shaping the phenotype of an individual developing within that environment, but also by shaping the phenotypes of its neighbouring conspecifics, whose demography and identities form part of that individual's external environment (Fig. 1; Dufty *et al.* 2002; Benard & McCauley 2008; Crean & Marshall 2009; Cote *et al.* 2010). Increasing evidence suggests nearby conspecifics serve as indicators of habitat quality and competitive environment. For example, Vercken *et al.* (2012) found that the ventral colour of neighbouring conspecifics motivates dispersal decisions of *Lacerta (Zootoca) vivipara* Jacquin lizards, as the relative abundance of specific colours corresponds with the relative prevalence of different competition strategies. However, in many studies of dispersal, individuals disperse with neighbours who have been raised under the same environmental conditions. For example, Crossman *et al.* (2011) found that downstream dispersal behaviours of

early-stage lake sturgeon larvae, *Acipenser fulvescens* Rafinesque, were influenced by whether their early development occurred in traditional or stream-side hatcheries. Studies such as these are remarkably useful in management and reflect that, in nature, many potential dispersers and their neighbours may come from the same developmental environment. However, these studies are unable to disentangle the degree to which individuals are acting based on their own phenotype or based on the phenotypes of the individuals around them, as both are likely shaped by their shared environment during development.

Here, we disentangled how juvenile environment mediates the influence of current environment on dispersal using the model system *Tribolium castaneum* Herbst (red flour beetles). Specifically, we induced two different dispersal phenotypes by exposing experimental individuals to either a low density or a high density of conspecifics as juveniles. We then allowed these two types of experimental individuals to disperse against a background of individuals that had experienced a common intermediate density of conspecifics as juveniles, and thus expressed a standardised phenotype. This novel approach allowed us to disentangle how juvenile environment influences dispersal via shaping phenotype directly (phenotype dependence) from how juvenile environment influences dispersal indirectly via shaping the phenotypes of the conspecific neighbours that form part of an individual's external environment (condition dependence).
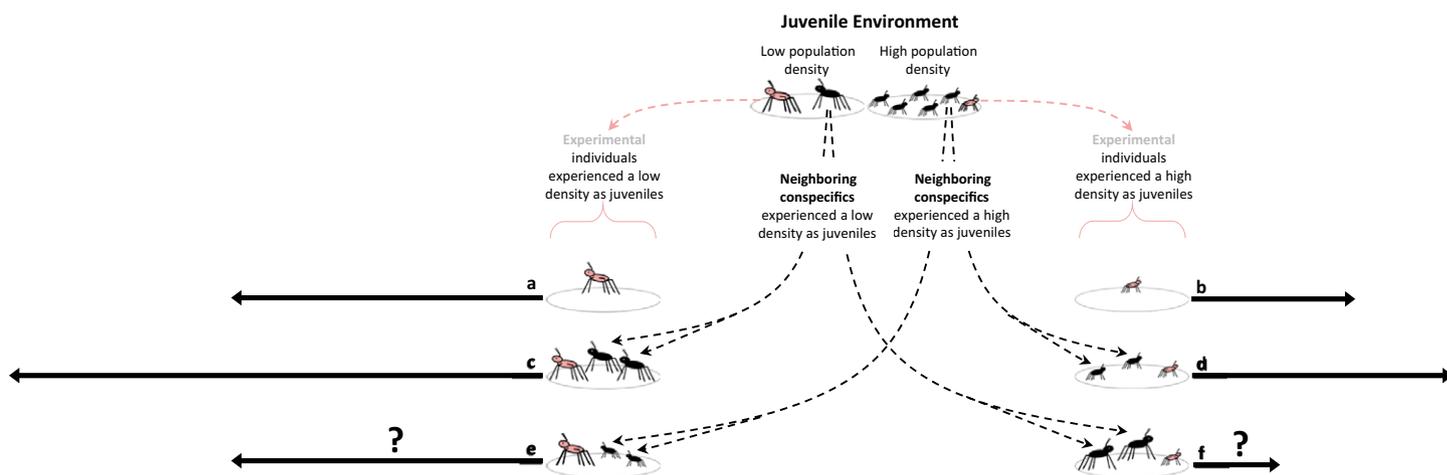
Figure 1 The above hypothetical scenario demonstrates how external condition and phenotype may interact to influence dispersal. Experimental individuals (in pink) develop larger bodies with longer legs when they experience a low population density (a less competitive environment) as juveniles rather than a high population density (a more competitive environment) as juveniles. As adults, experimental individuals are then introduced by themselves or with neighboring conspecifics (in black) into a habitat of standardized quality. Thick black arrows indicate the distance dispersed by the experimental individual, and thin dashed arrows represent an individual's juvenile environment. Here, phenotype influences how far individuals disperse (a ≠ b), as individuals move further when they are large than small (a > b). Dispersal is also influenced by external condition (a ≠ c, b ≠ d), as individuals disperse further when they detect neighbors than when dispersing alone (c > a, d > b). The effects of phenotype and external condition are non-additive, with experimental individuals dispersing especially far when they detect neighbors if the experimental individual experienced a low rather than a high population density as a juvenile ([c–a] > [d–b]). However, neighbors may influence dispersal not just by their presence, but also by their specific phenotypes. For example, individuals may disperse differently when the same number of neighbors are present, but those neighbors are large, not small (c ≠ e, d ≠ f). Studies of dispersal that investigate juvenile environment typically expose entire populations to the same experimental treatments, which means that individuals and their neighbors have a shared environmental history (such as c or d). Differences between treatments (c vs. d) may therefore be the result of juvenile environment either altering an individual's dispersal phenotype or altering their neighbors' phenotypes, thus changing an individual's external condition by altering their social environment. Standardizing the juvenile environment of neighbors therefore isolates how juvenile environment influences dispersal phenotypes (c vs. f, e vs. d), by disentangling this from the effect of how juvenile environment alters external condition via neighboring phenotypes.

We predicted that juvenile environment, due to its effect on phenotype, should determine how strongly individuals are influenced by external conditions (i.e. an interaction between phenotype dependence and condition dependence). For example, experimental individuals that experience a high density as juveniles may develop phenotypes that disperse far regardless of external conditions; high juvenile density could be a reliable indication that future competition will be high (Clobert *et al.* 2009), and thus select for adaptive plasticity that leads juveniles developing at high density to disperse to escape competition as adults. Alternatively, experimental individuals that experience a high density as juveniles may also develop phenotypes that disperse far, but only when external conditions are poor, as increased sensitivity to external condition may also be an adaptive response to poor external conditions as juveniles.

We also predicted that dispersal should be influenced by the juvenile environment of the neighbouring conspecifics that form part of a dispersing individual's external environment (i.e. condition dependence), and whose phenotypes are also shaped by juvenile environment. For example, experimental individuals that experience a high density as juveniles could induce their neighbours to disperse by giving cues that patch conditions are poor (Valone 1989; Danchin *et al.* 2004; Clobert *et al.* 2009) or alternatively could reduce dispersal by communicating to their neighbours that they are weak competitors.

MATERIALS AND METHODS

Study system

Tribolium castaneum (red flour beetle) is a well-established species for investigating patterns of dispersal that are likely common across diverse taxa (e.g. Naylor 1961; Campbell & Hagstrum 2002; Melbourne & Hastings 2009; Romero *et al.* 2009; Perez-Mendoza *et al.* 2011; Szűcs *et al.* 2014; Drury *et al.* 2016; Wexler *et al.* 2016). This system is particularly useful for investigating how phenotype dependence and condition dependence shape patterns of dispersal. First, both rearing densities and rearing habitat quality strongly shape the physical and behavioural phenotype of *T. castaneum* which, in turn, is known to influence dispersal (Perez-Mendoza *et al.* 2011; Van Allen & Rudolf 2013, 2016; Van Allen & Bhavsar 2014). For example, *Tribolium* beetles are typically smaller when reared in a low-quality than in a high-quality habitat (Van Allen & Rudolf 2013; Van Allen & Bhavsar 2014), which, among other phenotypic differences, alters how they disperse in response to current habitat quality and conspecific density (Van Allen & Bhavsar 2014). Second, by manipulating habitat quality and population size, we control whether *Tribolium* populations are above or below carrying capacity, providing clear, biologically relevant differences in external conditions. Third, we can standardise the age of individuals, a potentially confounding driver of dispersal (Cote *et al.* 2010). Fourth, we can divide the *Tribolium* life-cycle into two discrete stages in a laboratory setting: a juvenile stage constricting dispersal and an adult stage allowing dispersal. Discrete dispersal stages are a common attribute of many species (Moran 1994; McDougald *et al.* 2012) and allow juvenile

environment to be independent of the environment experienced during dispersal.

Rearing environment

Prior to the experiment, beetles were reared in colonies for at least 20 discrete, non-overlapping generations. For each generation, eggs were allowed 35 days to develop into mature adults, at which point they were allowed to oviposit eggs for the following generation. Colonies were maintained on large, high-quality patches of natal media (95% wheat flour, 5% brewer's yeast) and kept in incubators at 31°C and, on average, 54% humidity. We maintained two phenotypically distinct strains of *T. castaneum* (Kramer *et al.* 1984): a wild-type strain that is rust-red (hereafter: *experimental individuals*) and a strain homozygous for an allele that makes them distinctively black (hereafter: *standardised individuals*, because they formed the standardised background within which experimental beetles dispersed). Assigning experimental and standardised conditions (explained below) to visually distinctive strains allowed us to easily identify an individual's treatment status without tagging them.

Maternal effects are strong in *T. castaneum* (Van Allen & Rudolf 2013, 2016; Hufbauer *et al.* 2015). Thus, two generations prior to the experiment, we transitioned experimental beetles (generation 0; Fig. 2a) from their large colonies on high-quality, natal habitat to a harsher, novel habitat (98.85% corn flour, 1.0925% wheat flour, 0.0575% brewer's yeast) at a controlled number of 40 adult beetles during oviposition. This habitat was chosen to be intermediate in quality relative to the low-quality and high-quality environments used in the dispersal experiments described below and was used to reduce maternal carry-over effects from the high-quality, natal environment. At this time, standardised beetles were still maintained in their large colonies on high-quality, natal habitat (Fig. 2a).

To investigate how juvenile density influences dispersal, we next reared the experimental beetles at low and high population densities: 35 days after we allowed generation 0 to oviposit, the resulting cohort of experimental adults (generation 1; Fig. 2a) were allowed 24 hours to mate and oviposit either at a low population density ($n = 18$) or a high population density ($n = 90$) in new patches of the same, intermediate-quality habitat (98.85% corn flour). At this time, standardised beetles (generation 1) were introduced from their large colonies on high-quality, natal habitat to the same harsher, novel habitat used to mitigate maternal effects for the experimental beetles (98.85% corn flour, 1.0925% wheat flour, 0.0575% brewer's yeast) at a standardised intermediate population density ($n = 40$) during oviposition (Fig. 2a). The resulting mixed-sex, likely mated, cohorts of experimental and standardised adults (now 35 days old) were then used in our dispersal experiments.

Experimental design

We allowed populations of *T. castaneum* to disperse across replicate linear arrays, manipulating current density (low = 18 adults, high = 90 adults), current habitat quality (low = 99.5% corn flour, 0.475% wheat flour, 0.025% brewer's yeast; high = 98.2% corn flour, 1.71% wheat flour, 0.09% brewer's yeast)
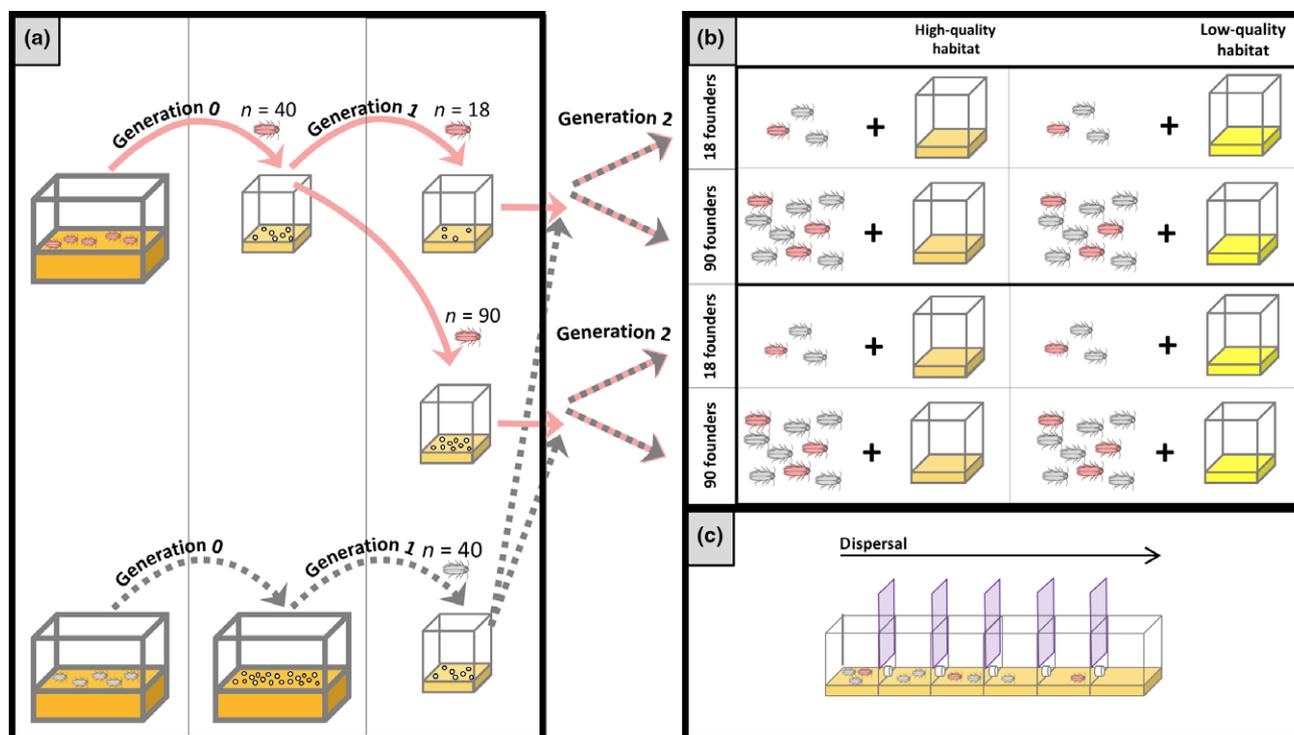
Figure 2 Time course and experimental design. Prior to the experiment, beetles were maintained in large panmictic colonies on large, high-quality patches of natal media (95% wheat flour, 5% brewer's yeast; see a, first column). Two generations prior to the experiment, we then standardised maternal effects; experimental beetles are shown in pink and standardised beetles are shown in grey (a). Pink and dotted grey arrows illustrate a 24-hour oviposition period for colonies of beetles (n = 18, 40 or 90). The resulting adults at the end of Generation 1 were used to establish populations at either a low (18 adults) or a high (90 adults) current density on habitat patches of either low or high quality (b). Each unique treatment combination was represented by 15–20 replicate dispersal arrays. Beetles were given 48 hours to acclimate to the first patch of a dispersal array before we lifted the gates and allowed them to disperse for 48 hours (c). To investigate how juvenile density influences how current density and habitat quality drive dispersal, we measured dispersal of both experimental and standardised beetles (represented in c by pink and grey beetles respectively) within each array. Recording the status (experimental or standardised) of each dispersing individual within each array also allowed us to address how standardised individuals are influenced by the environmental histories of their experimental neighbours.

and juvenile density (low and high, established prior to the experiment as described above) in a fully-factorial design (Fig. 2b; 2 current densities × 2 current habitat qualities × 2 juvenile densities × 15–20 replicate dispersal arrays = 143 arrays). One-third of beetles within each array were experimental beetles that experienced either a low or a high juvenile density (n = 18 or 90), while the remaining two-thirds of beetles were standardised beetles that experienced an intermediate juvenile density (n = 40). For example, in a low current density of 18 total beetles, six beetles were experimental and 12 beetles were standardised (overall this gave $2386_{experimental}$ + $4637_{standardised}$ = 7023 individuals). We chose habitat qualities such that for both low-quality and high-quality habitats, cohorts established at a low density were likely below carrying capacity (i.e. expected population growth rate $\lambda > 1$), while cohorts established at a high density were likely above carrying capacity (i.e. $\lambda < 1$) (based on data from Stewart *et al.* 2017, Fig. S1).

A total of 143 linear arrays were constructed out of 4 × 4 × 6 cm plastic boxes (hereafter: *patches*), which were held together by rubber bands and connected by 2 mm holes (following Melbourne & Hastings 2009; Szűcs *et al.* 2014; Szűcs *et al.* 2017; Weiss-Lehman *et al.* 2017). Linear arrays

contained either seven or nine patches (for the low or high current density treatments respectively) – enough patches, based on pilot runs, to ensure that individuals did not reach the last patch, and thus that dispersal was never limited by the length of the array. All 143 dispersal trials were conducted simultaneously. Half of the arrays were comprised of patches of low habitat quality, while the remaining half were comprised of patches of high habitat quality. Holes connecting patches were initially blocked by thin plastic sheets, which allowed beetles to acclimate for 48 hours in the first patch of a linear array. After the acclimation period, we simultaneously allowed the entire group of beetles to disperse among patches for 48 hours by lifting the sheets that blocked dispersal between patches. After 48 hours, we halted dispersal (by lowering sheets) and censused all experimental and standardised beetles within each patch of each array (Fig. 2c). We note that for some arrays, the number of individuals censused was not equal to the number of beetles released due to experimental error and/or mortality. Importantly, we treat different density levels as categorical (i.e. low vs. high) in our analyses; small deviations from densities therefore should not influence our results. We then used census data to characterise differences in dispersal kernels across treatment combinations.

Statistical analyses

We investigated dispersal by measuring how many patches individuals dispersed from their patch of origin (i.e. the first patch within the array) by the end of the 48-hour dispersal period. Thus, individuals that were censused in the second patch dispersed one patch, in the third patch dispersed two patches, etc. To evaluate whether juvenile environment mediates the effect of current density and habitat quality on dispersal across an array, we fit an ordinal regression with dispersal distance as the response variable using the *clmm* function in the *ordinal* package (version 2018.4.19, Christensen 2018) in R (version 3.5.0, R Core Team 2018). Ordinal regression was appropriate to fit our data as the maximum distance dispersed was only six patches and this model characterises the probability distribution of individuals across arrays, which accounts for differences in sample size across treatments (Bitume *et al.* 2013).

We analysed dispersal distance with individuals as the unit of replication. Fixed effects included current density (categorical: 18 or 90 adults), current habitat quality (categorical: low or high quality), juvenile density of experimental individuals (categorical: initiated with 18 or 90 adults), status (categorical: experimental or standardised) and all possible interactions. We included array as a random effect to account for non-independence of individuals within an array [model: distance dispersed ∼ current density × current habitat quality × juvenile density of experimental individuals × individual status + (1|array)]. The fixed effect of juvenile density represents an individual's own juvenile density for experimental individuals, but the juvenile density of one-third of an individual's neighbours for standardised individuals. We used nested likelihood ratio tests, following the principle of marginality, to assess the significance of model terms.

A significant main effect of current density or habitat quality would indicate that how far individuals disperse is influenced by their current environment (condition dependence). A significant main effect of juvenile density of experimental individuals or an interaction between juvenile density and status would indicate that how far individuals disperse is influenced by their phenotype (phenotype dependence). Significant interactions between juvenile density and either current density or habitat quality would indicate that phenotype, as induced by juvenile environment, influences how individuals respond to their current environment (i.e. an interaction between condition and phenotype dependence). Finally, a positive correlation between the dispersal behaviour of standardised and experimental beetles would indicate that how individuals disperse in response to external conditions is influenced not only by their own phenotype, but also by the phenotype of their neighbours (i.e. condition dependence based on social environment).

We then analysed five parameters of each dispersal kernel: mean, standard deviation, skew, kurtosis and maximum. We used a similar structure of fixed and random effects described above, but for linear mixed models instead of an ordinal logistic regression (see Table S1 for a detailed explanation). To standardise sample sizes across current density treatments, we averaged model results for each parameter from 1000 runs, with each run using a random draw of 12 individuals from

each dispersal array (six experimental, six standardised) (Table S1, as *per* Bitume *et al.* 2013).

RESULTS

Differences between our low-density and high-density juvenile treatments were biologically meaningful. As predicted, cohorts from low-density juvenile treatments were below carrying capacity ($\lambda = 1.39$) and cohorts from high-density juvenile treatments were above carrying capacity ($\lambda = 0.58$). Experimental individuals dispersed further than standardised individuals (main effect of status: $P < 0.0001$, Table 1; Table S1). Importantly, however, treatments had a similar effect on beetles of both statuses, as shown by a strong positive correlation between mean dispersal distance of experimental and standardised beetles within the same array (Fig. S2).

How far adults disperse is influenced by their current environment (condition dependence)

Current density strongly influenced the distribution of both experimental and standardised individuals across the linear arrays (Table 1; Figs. 3–5). Individuals, on average, were 21.4% more likely to emigrate (i.e. disperse from the first patch) when dispersing from a high-density than a low-density environment (Fig. 4). Individuals were also more likely to

Table 1 Results of the ordinal logistic regression testing for the effects of current density (18 or 90), habitat quality (low or high), juvenile density (low or high) and status (experimental or standardised) on the dispersal kernel of individuals across our linear, experimental arrays

	Experimental and Standardized Individuals		
	LR. stat	*P*-value	kernel parameters
Current density	**38.388**	**< 0.0001**	μ, ∨, σ
Habitat quality	3.013	0.083	μ
Juvenile density	0.123	0.726	
Status	**33.572**	**< 0.0001**	μ, ∨
Current density × habitat quality	**5.217**	**0.022**	μ
Current density × juvenile density	**8.330**	**0.004**	μ, ∨, σ
Habitat quality × juvenile density	2.451	0.118	
Current density × status	0.000	0.987	
Habitat quality × status	1.051	0.305	
Juvenile density × status	1.528	0.217	
Current density × habitat quality × juvenile density	0.2516	0.616	
Current density × habitat quality × status	0.0971	0.755	
Current density × juvenile density × status	0.0109	0.917	
Habitat quality × juvenile density × status	0.2356	0.627	
Current density × habitat quality × juvenile density × status	0.0116	0.914	

Predictors that have a significant effect on the dispersal kernel are in bold, and the specific parameters of the dispersal kernel that are significantly to marginally significantly influenced by the predictor ($P < 0.1$, see Table S1) are listed under 'kernel parameters' (μ = mean, ∨ = maximum, σ = standard deviation, γ = skew, and κ = kurtosis).
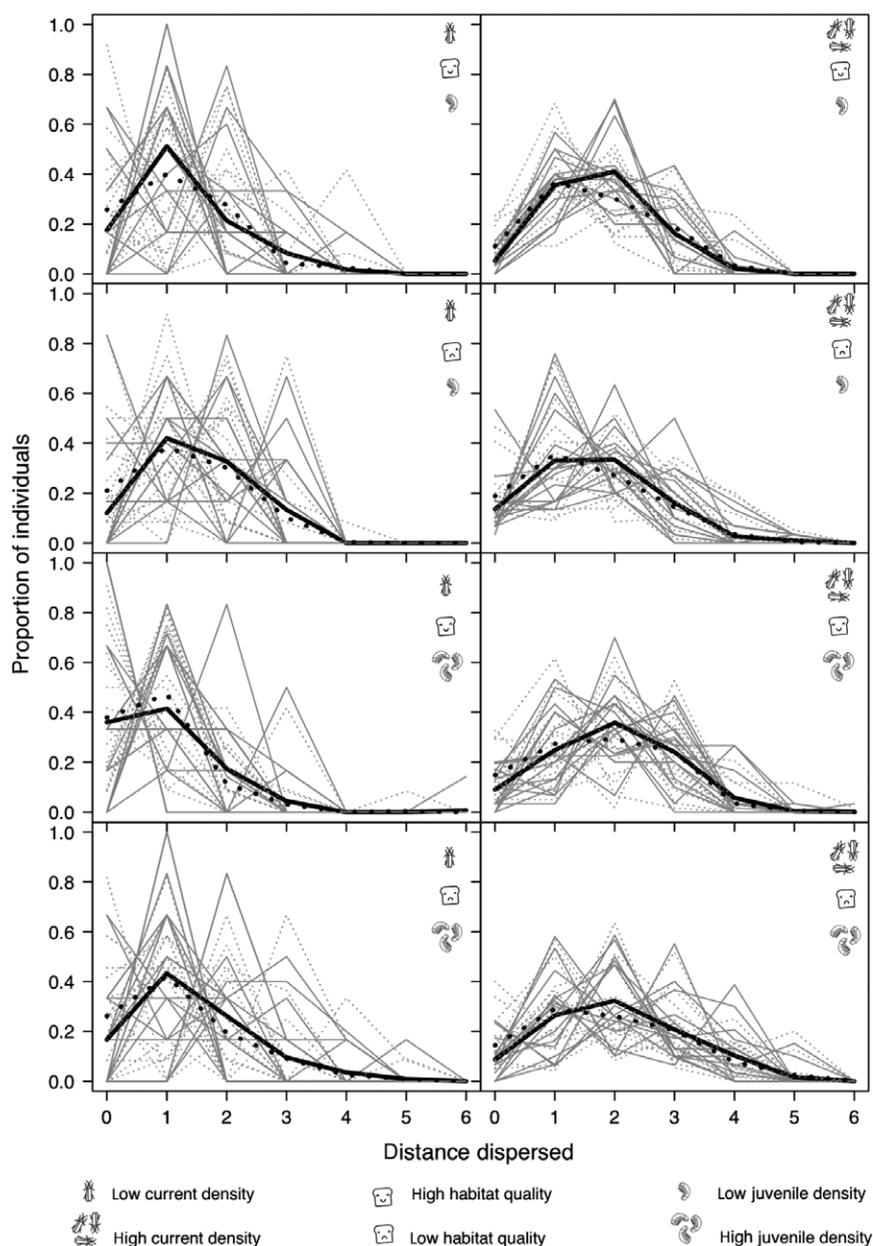
Figure 3 Dispersal kernels of treatment combinations for experimental and standardised individuals. Solid lines represent experimental individuals for each array and dotted lines represent standardised individuals for each array. Bold lines represent means for experimental and standardised individuals respectively. Current density, juvenile density and habitat quality treatment combinations are represented by symbols described in the legend.

disperse further (Table S1, Figs. 3 and 5, Fig. S3; significant effect on mean, standard deviation, maximum), while the shape of the dispersal kernel remained similar between high-density and low-density treatments (Table S1, no significant effect on skew or kurtosis; Fig. 3).

Habitat quality also mediated dispersal: individuals, on average, were more likely to disperse further (Fig. 3) in low-quality habitats than in high-quality habitats. This effect was largely driven by individuals established at a low current density, which, on average, dispersed further (Fig. 5, Table S1) when in low-quality than in high-quality habitats (Fig. 4a; current density by habitat quality interaction, $P = 0.022$). In contrast, individuals established at a high current density dispersed similarly across both habitat types (Figs. 4a and 5a).

How far adults disperse is influenced by their juvenile environment (phenotype dependence)

Juvenile density strongly mediated the effect of current density on dispersal (current density by juvenile density interaction, $P = 0.004$, Table 1). Specifically, individuals that experienced a low density as juveniles were, on average, 10.8% more likely to emigrate away from a high-density than a low-density environment (Fig. 4b). This effect was magnified for individuals that experienced a high density as juveniles (Fig. 4b) who were, on average, 33.1% more likely to emigrate and dispersed further when they experienced a high-density rather than a low-density environment as adults (Table S1). Juvenile density did not strongly
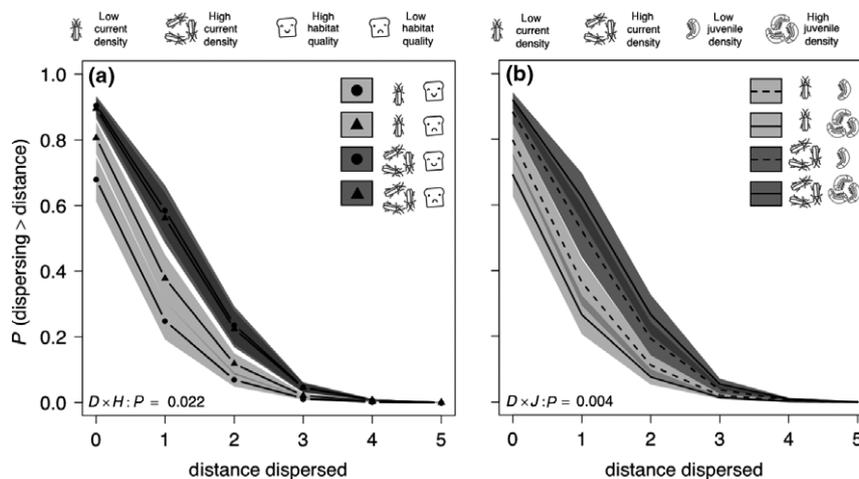
Figure 4 Decumulative probability distributions of all possible current density by habitat quality (a) and current density by juvenile density treatment combinations (b). On the *x*-axis, distance dispersed represents the number of patches from the origin (e.g. x = 0 represents the patch in which individuals were initially released, x = 1 represents the second patch in the array). On the *y*-axis, decumulative probabilities represent the probability that an individual will disperse further than the distance on the *x*-axis (e.g. the y-value at x = 0 is the probability of emigration, the y-value at x = 1 is the probability of dispersing at least as far as the third patch). Current density, juvenile density and habitat quality treatment combinations are represented by symbols described in the legend. The *P*-values represented in the lower, left-hand corner of each panel represent two-way interactions between current density (D) and either habitat quality (H) or juvenile density (J). Means and confidence intervals were extracted using *emmeans* version 1.2 in R (Lenth 2018).
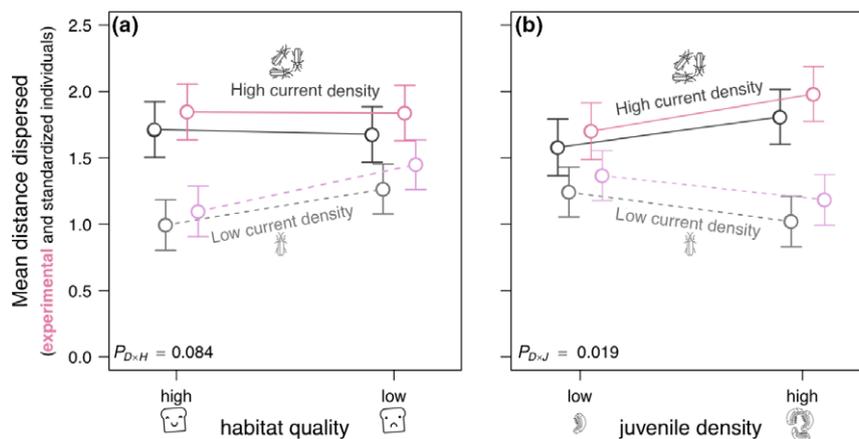
Figure 5 Average mean dispersal of experimental individuals (in pink) and standardised individuals (in grey) for current habitat and current density group combinations (a), as well as for current density and juvenile density group combinations (b). Y-values represent how many patches individuals have dispersed away from their initial habitat patch (e.g. the distance dispersed of individuals that remained in their initial patch was 0, while the distance dispersed of individuals that moved to the second patch was 1). Solid lines represent high current density treatments, while dashed lines represent low current density treatments. *P*-values indicate the average significance (see Supplement) for the interaction between current density and either current habitat quality or juvenile density (D × H or D × J, panels a or b respectively). Points are model means averaged across iterations and bars are 95% confidence intervals around model means averaged across iterations. Means and confidence intervals were extracted using *emmeans* version 1.2 in R (Lenth 2018).

mediate the effect of habitat quality on dispersal (habitat quality by juvenile density interaction, *P* = 0.118, Table 1, Fig. S4).

How far adults disperse is influenced by the phenotype of their neighbours (condition dependence based on social environment)

Individuals that experienced a high juvenile density dispersed further when released at high rather than at low density (current density by juvenile density interaction, *P* = 0.004, Table 1; Fig. 4b). Importantly, dispersal of standardised

individuals was consistently positively correlated with dispersal of experimental individuals, even across juvenile density treatments (Fig. S2). This not only suggests that experimental individuals were more likely to disperse when their phenotypes were shaped by a high rather than a low juvenile density, but also that standardised individuals were more likely to disperse when their *neighbours'* phenotypes were shaped by a high rather than a low juvenile density (Fig. 5b). Dispersal of standardised individuals was mediated by the juvenile environment, and thus the environmentally-induced phenotype, of their conspecific neighbours.

DISCUSSION

We provide strong evidence that juvenile environment shapes both phenotype-dependent and condition-dependent dispersal. In our experiment, individuals typically dispersed away from poor external conditions (i.e. condition dependence) and dispersed especially far away from poor external conditions if their phenotype was shaped by a high density as juveniles (i.e. the interactions between condition dependence and phenotype dependence represented by density × habitat [D × H] and density × juvenile environment [D × J] in Fig. 4; see also, Fig. 5). This suggests that external conditions are more likely to influence dispersal if individuals experienced a stressful rather than benign environment as juveniles. We found that dispersal also depends on juvenile environment, and thus phenotype, of neighbouring conspecifics. Specifically, individuals dispersed especially far away from a high density if just one-third of their neighbours' phenotypes were shaped by a high density as juveniles (Table 1). Therefore, the juvenile environment of even a small portion of a population can have a powerful impact on how the rest of that population disperses.

How far adults disperse is influenced by their current environment (condition dependence)

Increased dispersal at high densities is common across diverse taxa, as dispersers often escape competition (Bowler & Benton 2005; Matthysen 2005; Kubisch *et al.* 2014). Red flour beetles follow this pattern, as they exhibit negative density-dependent growth (Birch *et al.* 1951; Szűcs *et al.* 2014; Vahsen *et al.* 2018) and are more likely to disperse (Drury *et al.* 2016) and to disperse further (Szűcs *et al.* 2014) in low-quality than in high-quality habitats, and at a high rather than a low population density (Ziegler 1976).

Here, we confirm that both habitat quality and population density inform dispersal (Table 1; Fig. 4). Thus, cues from conspecifics and from resources appear to serve as distinct sources of information about the environment, which makes sense given that these two factors often jointly determine per capita resource availability (French & Travis 2001; Bowler & Benton 2005). However, while individuals exposed to a low density during dispersal were, as expected, more likely to disperse further in low-quality habitats than in high-quality habitats, individuals exposed to a high density during dispersal dispersed far regardless of their habitat quality (Fig. 4a). Cues indicating poor habitat quality may therefore be redundant if population density is high, as beetles already disperse far away from their initial patch. Understanding whether this finding has broader applicability for how species disperse will require further investigation. Some aspects of our design may have enhanced this effect in our study. For example, the difference between our density treatments may have been more challenging (e.g. in terms of their absolute effect on λ) than the difference between our habitat quality treatments. Future studies that investigate under what conditions cues are additive or redundant would provide greater insight into patterns in dispersal behaviour.

How far adults disperse is influenced by their juvenile environment (phenotype dependence)

The effects of environment on dispersal phenotypes can carry-over across discrete life history stages (Arambourou *et al.* 2017) and generations (Krug 2009; Crean & Marshall 2009; Meylan *et al.* 2012; Bitume *et al.* 2014; Van Allen & Bhavsar 2014; Van Allen and Rudolph 2016). Studies investigating how condition and phenotype dependence interact to influence dispersal are notable, yet relatively rare (Hansson *et al.* 2003; Chaput-Bardy *et al.* 2010; Selonen & Hanski 2010). The influence of juvenile environment on how far an individual disperses later in life remains even less well understood (Clobert *et al.* 2009; Wey *et al.* 2015).

Here, as predicted, we find that juvenile density has non-additive consequences for dispersal: individuals are more likely to disperse further away from a high current density rather than a low current density, but this difference is especially pronounced for individuals reared at a high rather than a low juvenile density. Juvenile environment can therefore alter how strongly individuals are influenced by external condition. Investigating the effects of juvenile environment is therefore imperative to refining our understanding of dispersal ecology, as it plays a key role in dispersal plasticity. Juvenile density in particular is important to understand. Density is already known to have lasting consequences for organismal phenotypes (Sinervo *et al.* 2000; Allen *et al.* 2008; Bitume *et al.* 2014; Betini *et al.* 2015), which likely translates into a strong effect on population spread.

Juvenile environment did not, however, strongly mediate how habitat quality influenced dispersal (Fig. S4). This may suggest that juvenile environment only induces individuals to better detect the external conditions that were challenging during their juvenile development. Alternatively, our density treatments may have been more stressful than our treatments for habitat quality. Future studies should investigate how juvenile environment changes condition dependence in other systems, and whether individuals are predisposed to disperse further away from poor external conditions that they also experienced as juveniles. Both of these topics are currently understudied but have strong implications for individual dispersal and population spread. In addition, studies that manipulate multiple variables during early development across a gradient of treatment levels would provide a stronger mechanistic understanding of these processes, especially if they document the specific traits responsible for altering dispersal behaviour.

How far adults decide to disperse is influenced by the phenotype of their neighbours (condition dependence based on social environment)

Neighbouring conspecifics are increasingly recognised as important sources of information, as their phenotypes may indirectly advertise habitat quality or competitive environment (Valone 1989; Boudjemadi *et al.* 1999; Danchin *et al.* 2004; Clobert *et al.* 2009; Vercken *et al.* 2012). For example, when individuals of the common lizard *Lacerta (Zootoca) vivipara* were prevented from dispersing earlier in the season, these 'frustrated' individuals influenced their conspecific neighbours

to disperse later in the season (Boudjemadi *et al.* 1999). Specific phenotypes may therefore indicate a poor environment and motivate neighbouring conspecifics to disperse. In contrast, individuals may also influence their neighbours if their past environment predisposes them to disperse further than their neighbours, and their neighbours simply follow the furthest disperser. For example, larva of the coral reef sponge *Luffariella variabilis* is more likely to settle in areas conditioned by earlier cohorts of conspecifics (Ettinger-Epstein *et al.* 2008).

Here, standardised individuals were more likely to disperse and to disperse further when their experimental neighbours' phenotypes were shaped by a high density rather than a low density during development. The phenotypes of experimental individuals exposed to a high density as juveniles are predisposed to disperse further in response to a high rather than a low density during dispersal, and standardised individuals mimicked their neighbours' dispersal (Fig. 5). Interestingly, the dispersal of standardised and experimental individuals is most strongly correlated when exposed to stressful external conditions during dispersal (Fig. S2). Individuals that experienced a high density as juveniles may have directly influenced their neighbours to disperse further, such as through aggressive behaviour, or may have indirectly influenced their neighbours to disperse by affecting their shared environment. Flour beetles in particular are known to secrete defensive chemicals that may either modify their environment (Markarian *et al.* 1978) or alter the behaviour of their neighbouring conspecifics, especially at high female densities (Khan *et al.* 2018). However, not all species use chemical cues to inform dispersal. For example, offspring of orange female *Lacerta (Zootoca) vivipara,* the common lizard mentioned above, disperse based on their preference for female conspecifics that are yellow, even when these females only comprise a minority of the population (Vercken et al. 2012). Regardless of the mechanism, our findings have strong implications for dispersal, as they suggest that the dispersal of an entire population can be driven by the environmental history experienced by a minority of the group.

While this is a biologically intuitive finding, there is a surprising dearth of evidence within the literature that the phenotype of a minority of individuals can shape the dispersal of an entire group. Studies that manipulate the composition of dispersing populations, such that individuals vary in their dispersal phenotypes (e.g. Fig. 1), therefore present a promising avenue of future research, as they could provide insight into what proportion of the population needs to have the same phenotype to effectively influence the dispersal of their neighbouring conspecifics. This refined understanding of what drives individual dispersal can be used to inform predictive models, allowing them to better capture the individual variation which, in part, makes predicting dispersal so difficult.

Ecological significance

Dispersal is strongly predictive of population spread (Fisher 1937; Skellam 1951; Levin *et al.* 2003; Kokko & López-Sepulcre 2006; Jongejans *et al.* 2008; Kubisch *et al.* 2014; Canestrelli *et al.* 2016), which means that understanding what influences dispersal is a key to better predicting and managing population expansion. In our experiment, current density and habitat quality influenced both the probability that individuals

would emigrate as well as the probability that individuals would continue to disperse to patches further along the array (Figs. 4 and 5). Patterns of individual dispersal therefore likely translate into lasting consequences for population-level processes. In addition, the three factors we manipulate here (current environment, habitat quality and juvenile environment) are all important drivers of rapid population spread (Grevstad 1999; Fagan *et al.* 2002; Theoharides & Dukes 2007; Liebhold & Tobin 2008; Catford *et al.* 2009; Wilson *et al.* 2009; Estrada *et al.* 2016). Promoting population spread is critical to managing or restoring threatened populations (Robinson and Handel 2000; Donald and Evans 2006). In addition, invasive species management relies on both hindering the spread of invaders as well as promoting the spread of agents released to control them (Fagan *et al.* 2002; With 2002; Theoharides & Dukes 2007; Liebhold & Tobin 2008).

CONCLUSION

Social environment is increasingly recognised as an important driver of dispersal. We find that how an individual disperses in response to its current surroundings depends on its phenotype. Individuals disperse away from poor external conditions, and how far they disperse depends on both their own phenotype, and the phenotype of neighbouring conspecifics. This finding has strong implications for dispersal ecology, as it suggests that an individual may influence the dispersal of an entire group, even if that individual's phenotype is in the minority. Incorporating the effect of past environment and current environment into studies of dispersal may therefore greatly strengthen the basic understanding of dispersal ecology.

AUTHORSHIP

SBE and MLV performed all analyses and wrote the first draft of the manuscript. SBE, MLV, JGM, KGT and RAH performed the experiment and helped to collect data. All the authors contributed to the experimental design, and significantly improved later drafts.

DATA ACCESSIBILITY STATEMENT

Data and R code available from Dryad Digital Repository: https://doi.org/10.5061/dryad.57qr203.

REFERENCES

Allen, R.M., Buckley, Y.M. & Marshall, D.J. (2008). Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *Am. Nat.*, 171, 225–237.

Arambourou, H., Sanmartin-Villar, I. & Stoks, R. (2017). Wing shape-mediated carry-over effects of a heat wave during the larval stage on post-metamorphic locomotor ability. *Oecologia*, 184, 279–291.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biol. Rev.*, 88, 310–326.

Benard, M.F. & McCauley, S.J. (2008). Integrating across life-history stages: consequences of natal habitat effects on dispersal. *Am. Nat.*, 171, 553–567.

Betini, G.A., Pardy, A., Griswold, C.K. & Norris, D.R. (2015). The role of seasonality and non-lethal carry-over effects on density-dependent dispersal. *Ecosphere*, 6, 272.

Birch, L.C., Park, T. & Frank, M.B. (1951). The effect of intraspecies and interspecies competition on the fecundity of two species of flour beetles. *Evolution*, 5, 116–132.

Bitume, E.V., Bonte, D., Ronce, O., Bach, F., Flaven, E., Olivieri, I. et al. (2013). Density and genetic relatedness increase dispersal distance in a subsocial organism. *Ecol. Lett.*, 16, 430–437.

Bitume, E.V., Bonte, D., Ronce, O., Olivieri, I. & Nieberding, C.M. (2014). Dispersal distance is influenced by parental and grand-parental density. *Proc. R. Soc. B Biol. Sci.*, 281, 20141061.

Bonte, D. & Dahirel, M. (2017). Dispersal: a central and independent trait in life history. *Oikos*, 126, 472–479.

Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M. et al. (2012). Costs of dispersal. *Biol. Rev.*, 87, 290–312.

Boudjemadi, K., Lecomte, J. & Clobert, J. (1999). Influence of connectivity on demography and dispersal in two contrasting habitats: an experimental approach. *J. Anim. Ecol.*, 68, 1207–1224.

Bowler, D.E. & Benton, T.G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.*, 80, 205–225.

Campbell, J.F. & Hagstrum, D.W. (2002). Patch exploitation by *Tribolium castaneum*: movement patterns, distribution, and oviposition. *J. Stored Prod. Res.*, 38, 55–68.

Canestrelli, D., Bisconti, R. & Carere, C. (2016). Bolder takes all? The behavioral dimension of biogeography. *Trends Ecol. Evol.*, 31, 35–43.

Catford, J.A., Jansson, R. & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.*, 15, 22–40.

Chaput-Bardy, A., Grégoire, A., Baguette, M., Pagano, A. & Secondi, J. (2010). Condition and phenotype-dependent dispersal in a damselfly, *Calopteryx splendens*. *PLoS One*, 5, e10694.

Christensen, R.H.B. (2018). Ordinal: Regression Models for Ordinal Data. R package version 2018.4.19. Available at: http://www.cran.r-project.org/package=ordinal/. Last accessed 08/22/2018.

Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S. & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.*, 12, 197–209.

Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M. (2012). *Dispersal Ecology and Evolution*. Oxford University Press, Oxford.

Clutton-Brock, T.H. & Lukas, D. (2012). The evolution of social philopatry and dispersal in female mammals. *Mol. Ecol.*, 21, 472–492.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 365, 4065–4076.

Crean, A.J. & Marshall, D.J. (2009). Coping with environmental uncertainty: dynamic bet hedging as a maternal effect. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 364, 1087–1096.

Crossman, J.A., Forsythe, P.S., Scribner, K.T. & Baker, E.A. (2011). Hatchery rearing environment and age affect survival and movements of stocked juvenile lake sturgeon. *Fish. Manage. Ecol.*, 18, 132–144.

Danchin, E., Giraldeau, L.A., Valone, T.J. & Wagner, R.H. (2004). Public information: from nosy neighbors to cultural evolution. *Science*, 305, 487–491.

Denno, R.F. & Roderick, G.K. (1992). Density-related dispersal in planthoppers – effects of interspecific crowding. *Ecology*, 73, 1323–1334.

Donald, P.F. & Evans, A.D. (2006). Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *J. Appl. Ecol.*, 43, 209–218.

Drury, D.W., Whitesell, M.E. & Wade, M.J. (2016). The effects of temperature, relative humidity, light, and resource quality on flight initiation in the red flour beetle, *Tribolium castaneum*. *Entomol. Exp. Appl.*, 158, 269–274.

Dufty, A.M., Clobert, J. & Moller, A.P. (2002). Hormones, developmental plasticity and adaptation. *Trends Ecol. Evol.*, 17, 190–196.

Estrada, A., Morales-Castilla, I., Caplat, P. & Early, R. (2016). Usefulness of species traits in predicting range shifts. *Trends Ecol. Evol.*, 31, 190–203.

Ettinger-Epstein, P., Whalan, S., Battershill, C.N. & de Nys, R. (2008). A hierarchy of settlement cues influences larval behaviour in a coral reef sponge. *Mar. Ecol. Prog. Ser.*, 365, 103–113.

Fagan, W.F., Lewis, M.A., Neubert, M.G. & van den Driessche, P. (2002). Invasion theory and biological control. *Ecol. Lett.*, 5, 148–157.

Fisher, R.A. (1937). The wave of advance of advantageous genes. *Ann. Eugen.*, 7, 355–369.

French, D.R. & Travis, J.M.J. (2001). Density-dependent dispersal in host-parasitoid assemblages. *Oikos*, 95, 125–135.

Gandon, S. (1999). Kin competition, the cost of inbreeding and the evolution of dispersal. *J. Theor. Biol.*, 200, 345–364.

Green, A.L., Maypa, A.P., Almany, G.R., Rhodes, K.L., Weeks, R., Abesamis, R.A. et al. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biol. Rev.*, 90, 1215–1247.

Grevstad, F.S. (1999). Factors influencing the chance of population establishment: implications for release strategies in biocontrol. *Ecol. Appl.*, 9, 1439–1447.

Hansson, B., Bensch, S. & Hasselquist, D. (2003). Heritability of dispersal in the great reed warbler. *Ecol. Lett.*, 6, 290–294.

Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S. & Bini, L.M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshw. Biol.*, 60, 845–869.

Hufbauer, R.A., Szűcs, M., Kasyon, E., Youngberg, C., Koontz, M.J., Richards, C. et al. (2015). Three types of rescue can avert extinction in a changing environment. *Proc. Natl. Acad. Sci. USA*, 112, 10557–10562.

Isles, A.R., Baum, M.J., Ma, D., Szeto, A., Keverne, E.B. & Allen, N.D. (2002). A possible role for imprinted genes in inbreeding avoidance and dispersal from the natal area in mice. *Proc. R. Soc. B Biol. Sci.*, 269, 665–670.

Johnson, J.C., Halpin, R., Stevens, D. II, Vannan, A., Lam, J. & Bratsch, K. (2015). Individual variation in ballooning dispersal by black widow spiderlings: the effects of family and social rearing. *Curr. Zool.*, 61, 520–528.

Jongejans, E., Skarpaas, O. & Shea, K. (2008). Dispersal, demography and spatial population models for conservation and control management. *Perspect. Plant Ecol. Evol. Syst.*, 9, 153–170.

Khan, I., Prakash, A., Issar, S., Umarani, M., Sasidharan, R., Masagalli, J.N. et al. (2018). Female density-dependent chemical warfare underlies fitness effects of group sex ratio in flour beetles. *Am. Nat.*, 191, 306–317.

Kokko, H. & López-Sepulcre, A. (2006). From individual dispersal to species ranges: perspectives for a changing world. *Science*, 313, 789–791.

Kramer, K.J., Morgan, T.D., Hopkins, T.L., Roseland, C.R., Aso, Y., Beeman, R.W. et al. (1984). Catecholamines and & β-alanine in the red flour beetle, *Tribolium castaneum*: roles in cutical sclerotization and melanization. *Insect Biochem.*, 14, 293–298.

Krug, P.J. (2009). Not my "type": larval dispersal dimorphisms and bet-hedging in Opisthobranch Life Histories. *Biol. Bull.*, 216, 355–372.

Kubisch, A., Holt, R.D., Poethke, H.-J. & Fronhofer, E.A. (2014). Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. *Oikos*, 123, 5–22.

Latham, N. & Mason, G. (2004). From house mouse to mouse house: the behavioural biology of free-living *Mus musculus* and its implications in the laboratory. *Appl. Anim. Behav. Sci.*, 86, 261–289.

Lenth, R. (2018). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.2. Available at: https://CRAN.R-project.org/package=emmeans. Last accessed 22 August 2018.

Leturque, H. & Rousset, F. (2002). Dispersal, kin competition, and the ideal free distribution in a spatially heterogeneous population. *Theor. Popul. Biol.*, 62, 169–180.

Levin, S.A., Muller-Landau, H.C., Nathan, R. & Chave, J. (2003). The ecology and evolution of seed dispersal: a theoretical perspective. *Annu. Rev. Ecol. Evol. Syst.*, 34, 575–604.

Liebhold, A.M. & Tobin, P.C. (2008). Population ecology of insect invasions and their management. *Annu. Rev. Entomol.*, 53, 387–408.

Markarian, H., Florentine, G.J. & Pratt, J.J. (1978). Quinone production of some species of *Tribolium*. *J. Insect Physiol.*, 24, 785–790.

Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography*, 28, 403–416.

Matthysen, E. (2012). Multicausality of dispersal: a review. In *Dispersal Ecology and Evolution*. (eds Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M.). Oxford University Press, Oxford, pp. 462–475.

McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H. *et al.* (2012). Seed dispersal in changing landscapes. *Biol. Cons.*, 146, 1–13.

McDougald, D., Rice, S.A., Barraud, N., Steinberg, P.D. & Kjelleberg, S. (2012). Should we stay or should we go: mechanisms and ecological consequences for biofilm dispersal. *Nat. Rev. Microbiol.*, 10, 39–50.

Melbourne, B.A. & Hastings, A. (2009). Highly variable spread rates in replicated biological invasions: fundamental limits to predictability. *Science*, 325, 1536–1539.

Meylan, S., Miles, D.B. & Clobert, J. (2012). Hormonally mediated maternal effects, individual strategy and global change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 367, 1647–1664.

Moran, N.A. (1994). Adaptation and constraint in the complex life-cycles of animals. *Annu. Rev. Ecol. Syst.*, 25, 573–600.

Naylor, A.F. (1961). Dispersal in red flour beetle *Tribolium castaneum* (Tenebrionidae). *Ecology*, 42, 231–237.

Palmqvist, E., Lundberg, P. & Jonzen, N. (2000). Linking resource matching and dispersal. *Evol. Ecol.*, 14, 1–12.

Perez-Gonzalez, J. & Carranza, J. (2009). Female-biased dispersal under conditions of low male mating competition in a polygynous mammal. *Mol. Ecol.*, 18, 4617–4630.

Perez-Mendoza, J., Campbell, J.F. & Throne, J.E. (2011). Effects of rearing density, age, sex, and food deprivation on flight initiation of the red flour beetle (Coleoptera: Tenebrionidae). *J. Econ. Entomol.*, 104, 443–451.

Poethke, H.J., Gros, A. & Hovestadt, T. (2011). The ability of individuals to assess population density influences the evolution of emigration propensity and dispersal distance. *J. Theor. Biol.*, 282, 93–99.

R Core Team (2018). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Last accessed 22 August 2018.

Robinson, G.R. & Handel, S.N. (2000). Directing spatial patterns of recruitment during an experimental urban woodland reclamation. *Ecol. Appl.*, 10, 174–188.

Romero, S., Campbell, J.F., Nechols, J.R. & With, K.A. (2009). Movement behavior in response to landscape structure: the role of functional grain. *Landscape Ecol.*, 24, 39–51.

Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.*, 38, 231–253.

Selonen, V. & Hanski, I.K. (2010). Condition-dependent, phenotype-dependent and genetic-dependent factors in the natal dispersal of a solitary rodent. *J. Anim. Ecol.*, 79, 1093–1100.

Sinervo, B., Svensson, E. & Comendant, T. (2000). Density cycles and an offspring quantity and quality game driven by natural selection. *Nature*, 406, 985–988.

Skellam, J.G. (1951). Random dispersal in theoretical populations. *Biometrika*, 38, 196–218.

Stewart, G.S., Morris, M.R., Genis, A.B., Szűcs, M., Melbourne, B.A., Tavener, S.J. *et al.* (2017). The power of evolutionary rescue is constrained by genetic load. *Evol. Appl.*, 10, 731–741.

Szűcs, M., Melbourne, B.A., Tuff, T. & Hufbauer, R.A. (2014). The roles of demography and genetics in the early stages of colonization. *Proc. R. Soc. B Biol. Sci.*, 281, 20141073.

Szűcs, M., Vahsen, M.L., Melbourne, B.A., Hoover, C., Weiss-Lehman, C. & Hufbauer, R.A. (2017). Rapid adaptive evolution in novel environments acts as an architect of population range expansion. *Proc. Natl Acad. Sci. USA*, 114, 13501–13506.

Theoharides, K.A. & Dukes, J.S. (2007). Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol.*, 176, 256–273.

Travis, J.M.J., Mustin, K., Barton, K.A., Benton, T.G., Clobert, J., Delgado, M.M. *et al.* (2012). Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods Ecol. Evol.*, 3, 628–641.

Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Barton, K., Bonte, D. *et al.* (2013). Dispersal and species' responses to climate change. *Oikos*, 122, 1532–1540.

Vahsen, M.L., Shea, K., Hovis, C.L., Teller, B.J. & Hufbauer, R.A. (2018). Prior adaptation, diversity, and introduction frequency mediate the positive relationship between propagule pressure and the initial success of founding populations. *Biol. Invasions*, 20, 2451–2459.

Valone, T.J. (1989). Group foraging, public information, and patch estimation. *Oikos*, 56, 357–363.

Van Allen, B.G. & Bhavsar, P. (2014). Natal habitat effects drive density-dependent scaling of dispersal decisions. *Oikos*, 123, 699–704.

Van Allen, B.G. & Rudolf, V.H.W. (2013). Ghosts of habitats past: environmental carry-over effects drive population dynamics in novel habitat. *Am. Nat.*, 181, 596–608.

Van Allen, B.G. & Rudolf, V.H.W. (2016). Carryover effects drive competitive dominance in spatially structured environments. *Proc. Natl Acad. Sci. USA*, 113, 6939–6944.

Vercken, E., Sinervo, B. & Clobert, J. (2012). The importance of a good neighborhood: dispersal decisions in juvenile common lizards are based on social environment. *Behav. Ecol.*, 23, 1059–1067.

Weiss-Lehman, C., Hufbauer, R.A. & Melbourne, B.A. (2017). Rapid trait evolution drives increased speed and variance in experimental range expansions. *Nat. Commun.*, 8, 14303.

Wexler, Y., Subach, A., Pruitt, J.N. & Scharf, I. (2016). Behavioral repeatability of flour beetles before and after metamorphosis and throughout aging. *Behav. Ecol. Sociobiol.*, 70, 745–753.

Wey, T.W., Spiegel, O., Montiglio, P.-O. & Mabry, K.E. (2015). Natal dispersal in a social landscape: considering individual behavioral phenotypes and social environment in dispersal ecology. *Curr. Zool.*, 61, 543–556.

With, K.A. (2002). The landscape ecology of invasive spread. *Conserv. Biol.*, 16, 1192–1203.

Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J. & Richardson, D.M. (2009). Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol. Evol.*, 24, 136–144.

Ziegler, J.R. (1976). Evolution of the migration response: emigration by *Tribolium* and influence of age. *Evolution*, 30, 579–592.

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