

Research



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Sex differences in dispersal syndrome are modulated by environment and evolution

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Dispersal syndromes (i.e. suites of phenotypic correlates of dispersal) are potentially important determinants of local adaptation in populations. Species that exhibit sexual dimorphism in their life history or behaviour may exhibit sex-specific differences in their dispersal syndromes. Unfortunately, there is little empirical evidence of sex differences in dispersal syndromes and how they respond to environmental change or dispersal evolution. We investigated these issues using two same-generation studies and a long-term (greater than 70 generations) selection experiment on laboratory populations of *Drosophila melanogaster*. There was a marked difference between the dispersal syndromes of males and females, the extent of which was modulated by nutrition availability. Moreover, dispersal evolution via spatial sorting reversed the direction of *dispersal* × *sex* interaction in one trait (desiccation resistance), while eliminating the sex difference in another trait (body size). Thus, we show that sex differences obtained through same-generation trait-associations ('ecological dispersal syndromes') are probably environment-dependent. Moreover, even under constant environments, they are not good predictors of the sex differences in 'evolutionary dispersal syndrome' (i.e. trait-associations shaped during dispersal evolution). Our findings have implications for local adaptation in the context of sex-biased dispersal and habitat-matching, as well as for the use of dispersal syndromes as a proxy of dispersal.

This article is part of the theme issue 'Linking local adaptation with the evolution of sex differences'.

1. Introduction

Many natural populations are spatially structured with some amount of dispersal across local habitats [1]. Environmental heterogeneity across these habitats can then lead to local adaptation [2], which allows the subpopulations to increase their average fitness in the context of their local environments. Dispersal plays a crucial role in this process and can either favour local adaptation by increasing the amount of available genetic variation or hinder it by introducing less adapted individuals to the population [3]. To complicate matters further, theory suggests that dispersal can interact in complex ways with other factors like genetic drift [4], genetic architecture [5] and environmental stochasticity [6] in shaping the local adaptation. Some of these insights have been empirically verified. For example, it has been shown that increasing the rate of migration enhances the rate of evolution for antibiotic resistance and reduces the associated costs in the bacterium *Pseudomonas aeruginosa* [7]. Similarly, the extent of local adaptation in parasite populations is determined by their migration rates relative to their hosts [8].

Another important way by which dispersal can potentially affect local adaptation is through its association with other phenotypic traits. Being a key life-history trait in individuals [9], dispersal typically has strong associations with other morphological, life-history or behavioural traits [10]. These trait associations with dispersal collectively comprise a 'dispersal syndrome' [11]

and affect the local adaptation in new environments [10,12] through the process of habitat matching [13,14]. Moreover, the capacity of subsequent movement by such dispersers would probably be modulated via the changes in their existing dispersal syndrome under the new environment. Consequently, dispersal syndromes have been extensively studied over the past two decades (reviewed in [11]). However, several important questions remain unanswered. For example, relatively little is understood about the patterns and consequences of sex differences in dispersal syndromes [15]. It is well known that several life-history and behavioural traits are significantly different across sexes in many taxa [16–18] and therefore it is reasonable to assume that dispersal syndromes would also vary across sexes. Both demographic and genetic effects of sex-biased dispersal (e.g. [19–21]) could amplify or weaken, if the two sexes have dissimilar dispersal syndromes due to differences in their physiology. Therefore, in species where both males and females disperse, sex differences in dispersal syndromes could play a major role in determining their local adaptation.

A general overview of the literature on dispersal syndromes indicates that a majority of the evidence for their existence comes from same-generation trait-association data, i.e. by comparing the traits of dispersive individuals with non-dispersive individuals (e.g. [22,23]). We call the dispersal syndromes inferred in this manner as ‘ecological dispersal syndromes’. However, it is not known whether these ecological dispersal syndromes allow us to make any predictions regarding the trait associations that take shape during evolution of dispersal (henceforth ‘evolutionary dispersal syndromes’). If an ecological dispersal syndrome could reliably predict the direction or extent of association between dispersal and other traits in the evolutionary dispersal syndrome (within the same environment), it would be a rich source of information on the heritable trade-offs involved with dispersal, besides being a good proxy of the dispersal status of individuals in the long-term. In contrast, an ecological dispersal syndrome that is incongruent with the evolutionary dispersal syndrome, even under the same environment, would be of limited utility. This becomes even more interesting in the context of the evolution of sex differences in dispersal syndrome. Depending on the exact nature of the selection pressure, males and females could also be differentially affected during dispersal evolution. For instance, if mating precedes dispersal but oviposition or giving birth follows dispersal, males and females might evolve very different resource allocation patterns. This is because, in such a scenario, for passing their genes to the next generation, the females have to undertake dispersal and pay its associated costs [24]. However, the males can potentially avoid dispersal, and hence the cost, by impregnating a large number of females prior to the latter’s dispersal. This sex-based divergence in strategies could result in a physiological adaptation for dispersal in females but not in males, leading to evolutionary differences in their dispersal syndromes. Thus, in principle, it is possible for dispersal syndromes to evolve differentially across sexes.

In this study, we investigated the dispersal syndrome in adult fruit flies, *Drosophila melanogaster*, as a composite of three traits: body size, desiccation resistance and exploratory tendency. Dispersers typically have larger body size across several taxonomic groups, *inter alia*, milkweed bugs [25], butterflies [26,27], birds [28–31] and mammals [31–33]. Stress

resistance is also likely to be positively associated with dispersal, as enduring hostile environments during the transition phase can be a beneficial trait for dispersers [34]. Similarly, exploratory tendency is expected to have a strong positive association with dispersal [12,35] as exploring the surrounding areas before initiating the journey is thought to be an integral part of the dispersal process [36]. Consequently, it is not surprising to find more exploratory individuals at the range margins [37] and in invasive species [12,38,39]. Unfortunately, the nature of sex differences in the context of dispersal is not well known for these traits (although see [40]). Therefore, we assessed the sex differences in dispersal syndrome of *D. melanogaster* by examining how body size, exploratory tendency and desiccation stress resistance varies in males and females between dispersers and non-dispersers. Specifically, we asked three questions: (i) Are dispersal syndromes in *D. melanogaster* sex-specific? (ii) How do sex differences in dispersal syndrome respond to a change in the environment (here, nutrition level)? (iii) How well are the evolutionary dispersal syndrome and its corresponding sex differences predicted by the ecological dispersal syndrome under the same environment?

To address these questions, we conducted three experiments. Experiment 1 involved the study of ecological dispersal syndrome under low nutrition, whereas Experiment 2 examined the ecological dispersal syndrome under standard nutrition. Experiment 3 assessed the evolutionary dispersal syndrome under standard nutrition. Thus, a comparison of data from Experiments 1 and 2 shows how an environmental factor (i.e. nutrient availability) modulates the sex differences in ecological dispersal syndrome, while a comparison of data from Experiments 2 and 3 shows how the sex differences differ between the ecological and evolutionary dispersal syndromes under a uniform environment. We found that dispersal syndromes are not only sex-specific, but these sex differences also vary across environments. We also show that the ecological and evolutionary dispersal syndromes differ substantially, with respect to both sex-independent and sex-specific effects.

2. Methods

(a) Fly populations

Large, outbred laboratory populations of *D. melanogaster* were used for all experiments. These populations trace their ancestry back to the IV lines, which were wild-caught at South Amherst, MA, USA in 1970 [41]. Ever since, these flies have been maintained in the laboratory at large population sizes (approx. 2400 individuals per population) to avoid inbreeding-like effects. A detailed description of the ancestry and maintenance regime of these fly populations is provided in electronic supplementary material, text S1.1 and S1.2, respectively. Flies from a population named DB₄ were used for investigating the ecological dispersal syndrome in Experiments 1 and 2. Populations DB_{1–4} also serve as the ancestors of populations VB_{1–4} (selected for higher dispersal) and VBC_{1–4} (corresponding control for VB₄) [42], which were used to assess the evolutionary dispersal syndrome. The ancestral relationship among the populations is outlined in electronic supplementary material, figure S1.

(b) Experiments

To identify flies as dispersive or non-dispersive individuals, we used two-patch dispersal set-ups, each comprising a source, a

path and a destination (similar to [42,43]). In this set-up, age-matched adult flies are introduced into a plastic container (source) that is connected to another empty plastic container (destination) via a long transparent plastic tube (path). The flies can thus disperse from the source to the destination, via the path. The path length and the time period allowed for dispersal can be varied as per the experimental requirements. This two-patch set-up has been used in the long-term dispersal selection experiment that gave rise to the aforementioned VB and VBC populations [42], as well as for investigation of density-dependent and sex-biased dispersal in *D. melanogaster* [43].

(i) Experiment 1: Ecological dispersal syndrome under low nutrition

For this experiment, approximately 38 000 eggs of the same age were randomly sampled from the DB₄ population and reared under low nutrition conditions (33%-diluted banana-jaggery medium, electronic supplementary material, text S1.4) in 640 vials, at a density of approximately 60 eggs/vial. Upon completion of their development into adults, we segregated these flies into dispersers and non-dispersers by subjecting them to three rounds of successive filtering, starting with 16 independent two-patch dispersal set-ups (electronic supplementary material, figure S2 and text S1.4). Through each of these dispersal rounds, flies that were consistently dispersive/non-dispersive were collected, while the rest were discarded. This ensured that we chose only those flies which showed a high repeatability [44,45] in their dispersive/non-dispersive behaviour. Dispersers and non-dispersers were then compared in terms of their life history and behaviour, to assess the ecological dispersal syndrome of flies under low nutrition.

(ii) Experiment 2: Ecological dispersal syndrome under standard nutrition

This experiment was identical to Experiment 1, with the sole exception that here, flies were reared under standard nutrition conditions (standard banana-jaggery medium, electronic supplementary material, text S1.5). Dispersers and non-dispersers were then segregated using three rounds of successive filtering (electronic supplementary material, figure S2 and text S1.5) and compared against each other to evaluate the ecological dispersal syndrome.

(iii) Experiment 3: Evolutionary dispersal syndrome under standard nutrition

For this experiment, we used VB (dispersal-selected) populations and their corresponding control and ancestral populations, VBCs ([42,46], see electronic supplementary material, figure S3 and text S1.6). At the time of this study, these flies had undergone selection for dispersal for 70 generations.

A potential way to investigate the evolutionary dispersal syndrome would be to compare the dispersers and non-dispersers within a given dispersal-selected population. That is, one could subject each VB population to similar kind of dispersal segregation as in Experiments 1 and 2, and then compare the dispersers and non-dispersers to assess the dispersal syndrome. However, there are two major problems with this approach. First, since VBs have undergone dispersal selection for 70 generations, it would be nearly impossible to obtain enough flies in these populations that do not disperse (i.e. non-dispersers). Second, during the course of dispersal evolution, there may have been some inadvertent selection for uncontrolled environmental variation acting on these populations, the effects of which would then get confounded with the effects of dispersal evolution.

In order to circumvent these issues, we used a different approach to assess the evolutionary dispersal syndrome. Like many other *Drosophila* life-history evolution experiments (for example, see [46,47]), we compared the VBs with their corresponding controls (VBCs), which have been maintained and evolved in parallel to these populations. Except for the selection for dispersal, the VBCs have undergone identical maintenance as the VBs (including the duration of desiccation stress faced by VBs during dispersal). Since Experiment 2 involved the ancestral population (DB₄) of VB₄ and VBC₄, the dispersal syndrome estimated therein would serve as an approximation of the dispersal syndrome at the beginning of the dispersal-selection experiment (where the flies were first sorted into dispersers and non-dispersers), whereas the dispersal syndrome assessed by comparing VBs and VBCs would serve as the evolutionary dispersal syndrome after 70 generations of selection. Before assessing the evolutionary dispersal syndrome via comparison of VBs and VBCs, all the populations were subjected to identical rearing conditions for one generation to eliminate any non-genetic parental effects.

(c) Dispersal syndrome traits

In all three experiments, the dry body weight of the flies was estimated in 10 batches of 20 males or 20 females from each of the treatments (dispersers/VB and non-dispersers/VBC), after drying at 60°C for 72 h (for details see electronic supplementary material, text S1.7.1).

For the desiccation resistance assay, we introduced 10 sets of 10 flies of either sex per treatment into empty transparent vials and monitored them every 2 h until death. The duration that each fly survived without food or moisture was scored as its desiccation resistance (electronic supplementary material, text S1.7.2).

Following an earlier assay set-up [48], exploratory tendency was measured by introducing individual flies into an enclosure formed by placing a Petri-plate lid (10-cm diameter, see [46] and electronic supplementary material, text S1.7.3) on a white paper. In this arena, the flies generally walk along the boundary of the enclosure and avoid venturing towards the open space in the centre [49]. Thus, the number of times a fly moves away from the boundary (beyond approximately 1 cm; following [48,49]) is taken as a measure of its exploratory tendency. Thirty-two flies of each sex were assayed from both dispersers and non-dispersers in Experiment 1 and 2. For Experiment 3, we used a part of an existing dataset [46], where the exploratory tendency of all dispersal-selected and control populations was measured identically as in Experiments 1 and 2.

(d) Statistical analyses

This study involved three experiments (1, 2 and 3), that were designed separately and conducted one after the other. In each experiment, we separately compared three traits (body size, desiccation resistance and exploratory tendency) across dispersers/non-dispersers (experiments 1 and 2) or VB/VBC (experiment 3). Among these, since Experiment 3 involved four blocks of dispersal-selected and control populations (VB₁₋₄ and VBC₁₋₄, respectively), the data for only the direct descendants of the DB₄ population (used in Experiments 1 and 2), i.e. VB₄ and VBC₄, were used whenever a comparison was made between Experiments 2 and 3.

One potential way to analyse the data for each trait would be to use three-way ANOVAs with experiment (1/2/3), dispersal (disperser/non-disperser) and sex (male/female) as fixed factors. In order to do this, we would have to use the data for only the direct descendants of the DB₄ population used in Experiments 1 and 2, i.e. VB₄ and VBC₄. This would allow us to directly test for the experiment × dispersal × sex interaction, thereby elucidating the effects of experiment (i.e. nutritional status or evolution) on how dispersal status interacts with sex. However,

if analysed this way, day-to-day environmental variations (since the three experiments were conducted on separate days) would be confounded with experiment identity, thereby increasing the noise in the data. This is the reason for which, in the *Drosophila* life-history literature, such experiments are typically performed with a blocked design, such that the effects of day-to-day variations can be explicitly accounted for using a mixed-model ANOVA (for example, see [46,47]). In the context of our study, that would mean that one replicate for each experiment (1/2/3) should have been performed on the same day, and this entire thing should have been repeated on multiple days to get the desired number of replicates. Unfortunately, this study was neither designed nor performed that way, thus rendering such a statistical analysis inappropriate. Thus, a better way to analyse these data would be to conduct separate ANOVAs for each trait in each of the three experiments with dispersal and sex as fixed factors (Experiment 3 would have an additional random factor of population block). This would allow one to compare the dispersers with the non-dispersers under each of the three experimental conditions. One can then qualitatively compare, say, the responses of the dispersers versus the non-dispersers in Experiment 1 with that of the dispersers versus the non-dispersers in Experiment 2 to assess the effects of nutrition on dispersal syndrome. The assumption here would be that if there are any systemic differences in the assay conditions (say changed atmospheric pressure [50]) across days, then they similarly affect the measured traits (i.e. body weight/desiccation resistance/exploratory tendency) of the dispersers and the non-dispersers. Unfortunately, although this statistical analysis better takes into account how the data were collected, it will not allow one to conduct the above-mentioned explicit statistical test for the experiment \times dispersal \times sex interaction for each of the three traits.

In this study, we analyse the same data in both the ways mentioned above. We believe that the analysis consisting of the separate experiment-wise ANOVAs is the more appropriate one, and present its results first. We then briefly present the analysis consisting of the pooled three-way ANOVAs and discuss its implications in §3c.

All the ANOVAs were carried out using STATISTICA v5 (StatSoft Inc. Tulsa, Oklahoma, USA). Tukey's HSD test was used to adjudge the pairwise differences between means, whenever a significant dispersal \times sex (or experiment \times dispersal \times sex) interaction was observed. Cohen's d was used as a measure of effect size for such significant differences, and the value of d was interpreted as large, medium and small for $d \geq 0.8$, $0.8 > d \geq 0.5$ and $d < 0.5$, respectively [51].

3. Results

As stated in §2d, the data were analysed in two different ways. Sections 3a and 3b present the results when, for a given trait, each experiment was analysed separately. Section 3c presents the results when data from all the experiments for a given trait were analysed using a pooled, three-way ANOVA.

(a) Sex differences in ecological dispersal syndrome varied under different nutrition levels

The results from two-way ANOVAs for Experiment 1 (low nutrition) and Experiment 2 (standard nutrition) were compared to qualitatively assess the differences in the ecological dispersal syndrome under the two nutrition regimes. The complete ANOVA tables are provided as electronic supplementary material, tables S1–S6.

Dispersers had a greater body weight than non-dispersers in both Experiment 1 ($p = 6.3 \times 10^{-7}$, $F_{1,36} = 36.38$) and

Experiment 2 ($p = 4.9 \times 10^{-5}$, $F_{1,36} = 21.21$). The dispersal \times sex interaction was not significant in Experiment 1 ($p = 0.71$, $F_{1,36} = 0.13$) (figure 1a), whereas in Experiment 2, there was a marginally significant dispersal \times sex interaction ($p = 0.06$, $F_{1,36} = 3.60$) (figure 1b). *Post hoc* tests for Experiment 2 revealed that the dispersive females were significantly heavier (Tukey's HSD, $p = 4.3 \times 10^{-4}$, $d = 1.7$) than non-dispersive females, whereas no such difference was observed for males (Tukey's HSD, $p = 0.24$).

For desiccation resistance, both experiments yielded a significant dispersal \times sex interaction (Experiment 1: $p = 3.9 \times 10^{-5}$, $F_{1,36} = 21.91$; Experiment 2: $p = 3.5 \times 10^{-6}$, $F_{1,36} = 29.99$) (figure 1d,e). While dispersive females were consistently more resistant to desiccation than non-dispersive females (Experiment 1: Tukey's HSD, $p = 1.6 \times 10^{-4}$, $d = 2.8$; Experiment 2: Tukey's HSD, $p = 1.6 \times 10^{-4}$, $d = 2.9$), no such trend was observed for males (Experiment 1: Tukey's HSD, $p = 0.93$; Experiment 2: Tukey's HSD, $p = 0.87$, also see figure 2).

The most discernible difference between low and standard nutrition conditions was observed for exploratory tendency. Experiment 1 revealed a significant dispersal \times sex interaction ($p = 0.01$, $F_{1,124} = 6.67$) (figure 1g). While dispersive males had significantly lower exploratory tendency than non-dispersive ones (Tukey's HSD, $p = 0.04$, $d = 0.6$), no such difference was observed in the female flies (Tukey's HSD, $p = 0.75$). In contrast, Experiment 2 showed neither a significant dispersal \times sex interaction ($p = 0.32$, $F_{1,124} = 0.98$) (figure 1h), nor a significant main effect for dispersal ($p = 0.56$, $F_{1,124} = 0.35$).

In summary, when the dispersers were compared with the non-dispersers in the context of a given experiment: (i) sex difference in body size was apparent under standard nutrition but not under low nutrition, (ii) sex difference in desiccation resistance was observed under both nutrition regimes, and (iii) sex difference in exploratory behaviour was apparent under low nutrition but not under standard nutrition.

(b) Evolutionary dispersal syndrome and the associated sex differences differed markedly from the ecological dispersal syndrome

To assess the differences in dispersal syndrome across different temporal scales (same-generation measurements versus post-dispersal evolution), results from individual ANOVAs for Experiment 2 and Experiment 3 were compared. The complete ANOVA tables are provided as electronic supplementary material, tables S1–S6.

While Experiment 2 revealed a marginally significant dispersal \times sex interaction as well as a main effect of dispersal on the body size (§3a), neither of these effects were found to be significant for Experiment 3. Dispersal-selected flies (VBs) had similar dry body weight as their controls (VBCs) ($p = 0.13$, $F_{1,3} = 4.30$), and dispersal did not show a significant interaction with sex ($p = 0.1$, $F_{1,3} = 5.56$) (figure 1c).

Interestingly, the pattern for desiccation resistance was completely reversed between the ecological and evolutionary dispersal syndromes. Dispersive females had a significantly greater desiccation resistance than their non-dispersive counterparts in Experiment 2 (§3a). In contrast, dispersal-selected flies in Experiment 3 had a lower desiccation resistance compared with the controls. Moreover, a significant dispersal \times sex response was observed ($p = 0.04$, $F_{1,3} = 10.99$)

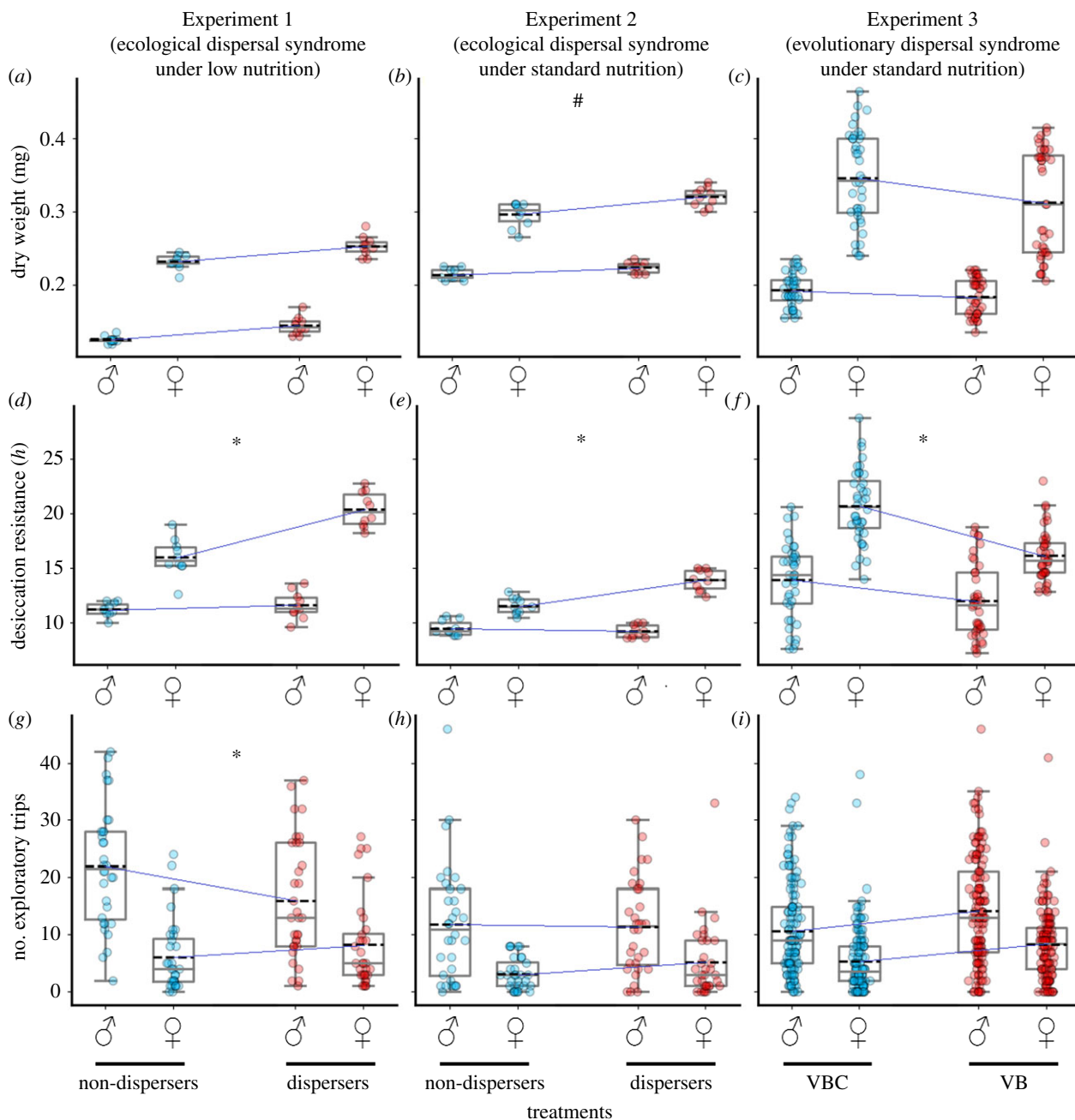


Figure 1. Dispersal \times sex interaction in the three experiments. Cleveland-box plots show male and female data for the three traits investigated (arranged row-wise in panels), across Experiments 1, 2 and 3 (arranged column-wise in panels). The circles (blue for non-dispersers/VBCs; red for dispersers/VBs) represent individual replicates, with a small random jitter along the x -axis. Box edges denote 25th and 75th percentiles, while the black solid and broken lines represent the median and mean, respectively. Asterisk denotes $p < 0.05$ for the dispersal \times sex interaction, whereas hash sign denotes $0.05 < p < 0.1$ for the dispersal \times sex interaction. For the exact p values of ANOVA, refer to electronic supplementary material tables S1, S3 and S5. For the p values of pairwise differences (Tukey's HSD test), refer to electronic supplementary material, tables S2, S4 and S6.

(figure 1*f*) in Experiment 3, although dispersal-selected flies of both sexes had a significantly lower desiccation than the corresponding control flies (Males: Tukey's HSD, $p = 1.2 \times 10^{-5}$, $d = 0.6$; Females: Tukey's HSD, $p = 7.7 \times 10^{-6}$, $d = 2.0$). This was probably due to the larger magnitude of difference in females than in males (figures 1*f* and 2).

For exploratory tendency, while Experiment 2 did not show a significant effect of dispersal (§3a), Experiment 3 revealed a significant main effect of dispersal ($p = 0.04$, $F_{1,3} = 11.96$). The dispersal-selected flies had a higher exploratory tendency in both sexes, and the dispersal \times sex interaction was not significant ($p = 0.93$, $F_{1,3} = 0.01$) (figure 1*i*).

Thus, the evolutionary dispersal syndrome differed substantially from the ecological dispersal syndrome, in terms

of both sex-independent and sex-specific effects. It should be noted here that while assessing the ecological dispersal syndrome in Experiment 2, the dispersers and non-dispersers belonged to the same population (i.e. DB₄). On the other hand, while investigating the evolutionary syndrome, a given pair of dispersers (VBs) and non-dispersers (VBCs) belonged to two different populations, both of which were descendants from a common DB population (§2a).

(c) Analysing the three experiments together

In this pooled analysis, data were considered from only VB₄ and VBC₄ populations (i.e. the direct ancestors of DB₄ population), to lend symmetry to the ANOVA design. The complete

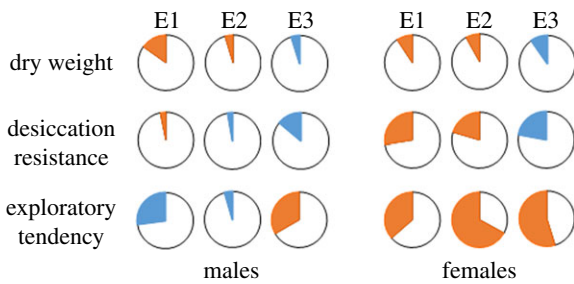


Figure 2. Dispersal syndromes of males and females in the three experiments. E1, E2 and E3 represent Experiments 1, 2 and 3, respectively. Area of the coloured sector in the circles represents the percentage difference in the corresponding trait value for dispersers (for E1 and E2) or VBs (for E3), with respect to the non-dispersers and VBCs, respectively. Orange and blue colours denote positive and negative changes, respectively, in the dispersers (or VBs). It can be noted that the overall dispersal syndrome differs between males and females. Furthermore, this sex difference in dispersal syndromes varies across the three experiments. For exact values of the effect size (Cohen's d) associated with these differences, refer to electronic supplementary material, tables S2, S4 and S6.

ANOVA tables are provided as electronic supplementary material, tables S7–S11.

Three-way ANOVA for the body weight data pooled over the three experiments yielded a significant experiment \times dispersal interaction ($p = 3.5 \times 10^{-6}$, $F_{2,108} = 14.13$), whereas the dispersal \times sex and experiment \times dispersal \times sex interactions were not significant ($p = 0.50$, $F_{1,108} = 0.46$, and $p = 0.15$, $F_{2,108} = 1.96$, respectively).

In contrast, for desiccation resistance, all the tested effects, including experiment \times dispersal ($p < 10^{-6}$, $F_{2,108} = 94.24$), dispersal \times sex ($p = 0.007$, $F_{1,108} = 7.64$) and experiment \times dispersal \times sex ($p = 7.1 \times 10^{-7}$, $F_{2,108} = 16.18$), were found to be significant.

For exploratory tendency, the effect of experiment \times dispersal ($p = 0.18$, $F_{2,372} = 1.71$) was not significant, but the dispersal \times sex interaction was significant ($p = 0.04$, $F_{1,372} = 4.40$). Further, The experiment \times dispersal \times sex interaction was marginally significant ($p = 0.06$, $F_{2,372} = 2.75$).

The presence of an experiment \times dispersal \times sex interaction in two of the three traits studied indicates that sex differences in dispersal syndrome were being affected differently across the three experiments. The *post hoc* results for these traits are provided in electronic supplementary material, tables S9 and S11. In summary, this analysis (along with the *post hoc* results) shows that while significant sex-specific differences were observed in desiccation resistance, these differences were not significant for exploration and body size. This outcome is not surprising as this analysis confounds the effects of experimental treatments with day-to-day variations, thereby increasing the amount of noise in the data. Therefore, we refrain from interpreting the results of these pooled, three-way ANOVAs. We report them here solely for the sake of comprehensiveness.

4. Discussion

(a) Dispersal syndromes in *D. melanogaster* are sex-specific

In sexually dimorphic species, the associations among life-history traits are often sex-specific [17]. However, despite the increasing realization that dispersal is a key life-history

component [9], sex differences in dispersal syndromes remain poorly understood. This is even more surprising in light of the fact that sex differences in dispersal traits (i.e. sex-biased dispersal) are quite ubiquitous and well-studied, both empirically and theoretically (reviewed in [52,53]). Comparing the traits of dispersers and non-dispersers, we show that the dispersal syndrome in *D. melanogaster* differs substantially between males and females (figure 2). Across the three experiments, these sex differences were apparent in the life-history traits (body size and desiccation resistance) as well as the behavioural trait (exploratory tendency) (figure 1). As the environment is a crucial determinant of ecological trait-associations [54], we next investigated whether and how the sex differences in dispersal syndrome vary across environments.

(b) Nutrition level can modulate the sex differences in dispersal syndrome

Any ecological trait association is likely to change in the face of environmental shifts. This is also expected in the case of dispersal syndromes [11,55], and recent studies have devoted much effort to delineating the contributions of genetic and environmental factors in shaping the dispersal syndromes, most notably in butterflies [15,56]. However, it is not known how sex differences in dispersal syndromes respond to environmental changes.

Comparing the results from Experiments 1 and 2, we show that the pattern of sex differences in *Drosophila* dispersal syndrome varied across the two nutritional regimes (figure 2), quite interestingly, in different directions for different traits. Low nutrition obscured the existing sex difference in body size (cf. figure 1*a* and 1*b*), maintained the sex difference in desiccation resistance (cf. figure 1*d* and 1*e*), and uncovered a sex difference in exploratory tendency (cf. figure 1*g* and 1*h*). While sex differences in life-history traits have already been shown to change with nutrition availability [57], the observation that diet changes sex differences in a behavioural trait (exploratory tendency) is novel to the best of our knowledge. In addition to supporting the already established notion that nutrition levels influence overall behaviour [58,59], it demonstrates the effect of nutrition on the sex differences in behaviour.

In terms of body size, we found that dispersers of both sexes were larger than non-dispersers in Experiment 1 (figure 1*a*), which is consistent with the results of trait-association studies across taxa [25,31], including *D. melanogaster* [60]. In terms of desiccation resistance, the female dispersers fared better than their non-dispersive counterparts in both nutritional regimes, whereas males showed similar desiccation resistance irrespective of their dispersal status (figure 1*d,e*). The exploratory tendency of dispersers was not higher than that of the non-dispersers in any of the nutritional regimes or sexes, indicating that exploratory tendency was not an essential prerequisite for successful dispersal in our experimental set-up. This is unexpected because even in our set-up, the flies had to locate the single aperture in the source through exploration (i.e. there were no cues that guided them towards the exit). The lack of greater exploratory tendencies in the dispersers is also in contrast with most of the literature on personality-dependent dispersal, where behaviours such as exploration are expected to confer an advantage during dispersal [35,55]. More surprisingly,

dispersive males even showed a lower exploratory tendency than non-dispersive males under low nutrition (figure 1g). In short, although environment is known to play a crucial role in the shaping of dispersal syndrome [56], we show that the pattern of sex differences in dispersal syndrome can vary across different environmental contexts (here, nutrition level), with possibilities ranging from obscuring of existing sex differences to appearance of new ones (figure 2). Hence, care must be taken while extrapolating observed dispersal syndromes as well as any underlying sex differences to other environmental conditions.

Over long time scales, same-generation trait associations are liable to change in three ways: first, due to changes in the environment alone; second, via evolutionary changes in the populations; and finally, through an interaction of the two mechanisms. Understandably, it is quite difficult to disentangle these three causes of changes in dispersal syndrome in natural populations. To address the issue of changed environments confounding the possible effects of phenotypic evolution, we next investigated the evolutionary dispersal syndrome using dispersal-selected populations that have been maintained under identical laboratory conditions of light and temperature as Experiments 1 and 2, and selected using the same dispersal set-up that was used for segregation of dispersers/non-dispersers in Experiments 1 and 2. Furthermore, the flies in the evolved populations were reared under standard nutrition (as in Experiment 2), and were assayed under conditions identical to those in Experiments 1 and 2. Thus, using highly controlled and reproducible laboratory conditions, we sought to remove the effects of environment as a confounding factor as much as practicable.

(c) Ecological and evolutionary dispersal syndromes can differ substantially, even under similar environmental conditions

The notion that ecological dispersal syndromes, obtained from same-generation association studies, can potentially predict the trait associations after dispersal evolution [11] has never been investigated empirically. Here, we investigated the sex-specific changes in dispersal syndrome due to dispersal evolution by comparing the dispersal syndromes among males and females of dispersers and non-dispersers in Experiments 2 with the corresponding syndromes of males and females of selected and control populations in Experiment 3. In Experiment 2, we found a sex-specific difference of dispersal syndrome in terms of body size, with dispersers being significantly larger only in females but not in males. However, Experiment 3 revealed that the body size of the males and females of the dispersal selected populations were not different from the males and females of the VBCs (figure 1c; electronic supplementary material, table S1), thus suggesting a change in the pattern of sex-specific dispersal syndrome. More critically, contrary to the expectations from literature [25,31,60], neither males nor females in dispersal-selected populations had a greater body size than the corresponding controls. One potential reason for this might be the fact that under our standard nutrition, the flies have access to *ad libitum* resources at any given point, and therefore do not need to acquire and store greater amount of resources in the body. This automatically leads to the prediction that if selection for dispersal were to

happen under nutrient-limited condition, the dispersal syndrome with respect to body size might be very different.

For desiccation resistance, a number of interesting and contrasting observations were obtained in Experiment 3. First, contrary to the ecological dispersal syndrome (Experiment 2, figure 1e), desiccation resistance of the dispersal-selected flies (VBs) was significantly lower than corresponding controls (VBCs) for both sexes. This suggests that, at an evolutionary time scale, dispersal traded-off with desiccation resistance. Second, although the *dispersal* \times *sex* interaction was significant in Experiment 3, the direction had reversed completely, i.e. there was a reduction in desiccation resistance of VBs, which was more apparent in females than in males (cf. figure 1e and 1f, electronic supplementary material, table S4). Third, despite having a comparable body size, the desiccation resistance of VBs was significantly lower compared with the VBCs. This contradicts a well-documented positive correlation between body size and desiccation resistance [61,62]. These observations make sense when we note that VBs have evolved significantly greater levels of locomotor activity [42]. The constitutively higher activity of the VB flies is likely to exhaust them faster in the absence of food and moisture, thus making them more susceptible to desiccation stress, particularly given that their body size is comparable to that of VBC flies (figure 1c).

Differences between the ecological and evolutionary dispersal syndromes were also observed for exploratory tendency, a key component of behavioural syndromes and personalities in animals [35,55]. There was no difference between dispersers and non-dispersers in Experiment 2, whereas dispersal-selected flies of both sexes in Experiment 3 evolved a significantly higher exploratory tendency (figure 2; electronic supplementary material, table S5). This is in accordance with the results of studies on natural populations reporting the presence of more exploratory individuals at range-expansion fronts [37] and in invasive species [38,39].

Together, these results highlight that the short-term association of traits observed in same-generation studies (i.e. ecological dispersal syndrome) may not be a good predictor of the long-term evolutionary changes (i.e. evolutionary dispersal syndrome), even if the environment remains relatively unchanged.

There are two potential reasons for this observation. First, in addition to the obvious role played by additive genetic variance, the non-additive components of genetic variance and environmental effects could play a role in shaping the same-generation phenotypic correlations. However, during the course of evolution, only the heritable components of the phenotypic variation get transmitted to the future generations. The evolution of correlated traits is also shaped by phenomena such as pleiotropy and linkage disequilibrium. Second, there is a theoretical possibility of some uncontrolled environmental variation acting on the dispersal-selected and control populations which could contribute to the divergence between ecological and evolutionary dispersal syndromes. However, given that environments under laboratory conditions are tightly controlled, such a situation is extremely unlikely.

The idea that same-generation phenotypic associations may not always be a good predictor of the direction of evolutionary responses has been empirically examined before [63]. However, it had never been tested in the context of dispersal syndromes or their sex differences.

While studies on dispersal syndromes have discussed the labile nature of dispersal syndromes in the face of evolution [11], the focus has mostly been on the effect of changing environments during the course of evolution [15]. By demonstrating the differences in ecological and evolutionary dispersal syndromes under a uniform environment, we show that such evolutionary predictions are risky even when environments do not change during evolution.

(d) Implications for local adaptation

We demonstrate that not only can there be sex differences in dispersal syndromes, but they can also reorient owing to environmental changes (here, low nutrition) as well as dispersal evolution by spatial sorting. These findings have several implications in the context of ecological and evolutionary role of dispersal in determining the degree of local adaptation. First, sex differences in dispersal syndromes can lead to indirect demographic consequences. For instance, various studies have reported positive, negative or no correlation of dispersal with body size [31,64], mating success [65–67] and fecundity [24,68], traits that have major effects on the temporal dynamics of populations. Sex-specific variations in these traits would further affect the dynamics of populations that are connected by migration (i.e. metapopulations) [69]. While this kind of non-random (i.e. phenotype-dependent) gene flow across populations has been recently recognized in the context of dispersal syndromes [55], this observation has not yet been made in the context of syndromic sex differences, probably because of the lack of empirical evidence for the latter. Second, like any other phenotype-dependent dispersal event [70], sex-specific dispersal syndromes can also

have evolutionary consequences. In fact, behavioural syndromes have already been suggested to have sexually dimorphic fitness consequences, including the possibility of generating evolutionary conflict between males and females [71]. In addition to such individual-level effects, sex differences in dispersal syndromes would also modulate the degree of habitat-matching in the newly colonized areas, with potential evolutionary consequences for source-sink dynamics [72] as well as functioning of metacommunities [14]. Finally, this study reinforces the lability of dispersal syndromes across both environments (Experiments 1 and 2) and evolutionary time scales (Experiments 2 and 3), thus calling into question their utility as predictors of dispersal.

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.4cn693k>

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