

Desiccation Stress Acts as Cause as well as Cost of Dispersal in *Drosophila melanogaster*

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ABSTRACT: Environmental stress is one of the important causes of biological dispersal. At the same time, the process of dispersal itself can incur and/or increase susceptibility to stress for the dispersing individuals. Therefore, in principle, stress can serve as both a cause and a cost of dispersal. We studied these potentially contrasting roles of a key environmental stress (desiccation) using *Drosophila melanogaster*. By modulating water and rest availability, we asked whether (a) dispersers are individuals that are more susceptible to desiccation stress, (b) dispersers pay a cost in terms of reduced resistance to desiccation stress, (c) dispersal evolution alters the desiccation cost of dispersal, and (d) females pay a reproductive cost of dispersal. We found that desiccation was a clear cause of dispersal in both sexes, as both male and female dispersal propensity increased with increasing duration of desiccation. However, the desiccation cost of dispersal was male biased, a trend unaffected by dispersal evolution. Instead, females paid a fecundity cost of dispersal. We discuss the complex relationship between desiccation and dispersal, which can lead to both positive and negative associations. Furthermore, the sex differences highlighted here may translate into differences in movement patterns, thereby giving rise to sex-biased dispersal patterns.

Keywords: dispersal propensity, desiccation resistance, life history, dispersal syndrome, fecundity, movement ecology, dispersal evolution, spatial selection.

Introduction

Biological dispersal is often driven by numerous biotic and abiotic causes that promote movement across space (Matthysen 2012). However, the process of movement can be costly to the dispersing organisms in several ways (Bonte et al. 2012). Investigating the causes and costs of dispersal can therefore help us understand the constraints faced by individual organisms (Ronce and Clobert 2012), as well as their potential effects on the population- and community-level consequences of dispersal (Bowler and Benton 2005).

Since dispersal is a key life history trait in individuals (Bonte and Dahirel 2017), one possible way to decipher its causes and costs is by studying dispersal syndromes, that is, the covariation of dispersal with other life history and behavioral traits (Ronce and Clobert 2012). Such dispersal syndromes have been documented in various insects (Dingle 1974; Legrand et al. 2016; Tung et al. 2018a), as well as in other terrestrial (Stevens et al. 2014) and aquatic (Comte and Olden 2018) animals. While these trait correlations can help us understand the underlying physiological mechanisms and constraints of dispersal, they are often contingent on the study environment and population history. This is because trait associations change rapidly and significantly if the environment changes or if the population undergoes evolutionary changes (Chippindale et al. 2003; Jessup and Bohannan 2008; Mishra et al. 2018a). Moreover, dispersal may be modulated by many causes at once (Matthysen 2012; Legrand et al. 2015) and incur several simultaneous costs to the individuals (Roff 1977; Gros et al. 2008; Bonte et al. 2012). Taken together, this makes a thorough investigation of dispersal-trait associations difficult under natural conditions. Therefore, one possibility is to study populations with a known history under a simplified environment to understand how a particular trait association (and hence the dispersal syndrome) is shaped.

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Desiccation stress is one of the factors that can greatly influence dispersal. It is not only one of the most commonly faced environmental stress for numerous taxa (Black and Pritchard 2002; Holmstrup et al. 2002; Kranner et al. 2008; Holzinger and Karsten 2013) but also is one of the first signs of an unfavorable environment, as the stress due to lack of water sometimes precedes a lack of other resources, such as food (Karan and Parkash 1998; Hoffmann and Harshman 1999). Understandably, desiccation not only affects the physiology of individual organisms (e.g., Folk and Bradley 2004; Bazinet et al. 2010) but also is an important determinant of species distributions (e.g., Gibbs et al. 1997; Kellermann et al. 2009; Rajpurohit et al. 2013). Furthermore, organisms' responses to desiccation stress are particularly important in the context of climate change and its biological implications (Hoffmann et al. 2003; Tuba et al. 2011; Van Heerwaarden and Sgrò 2014; Wang et al. 2021). Given that dispersal often serves as the first line of defense against unfavorable environments for many taxa (Gerber and Kokko 2018; Riotte-Lambert and Matthiopoulos 2020), investigating the relationship between movement and desiccation stress can inform our understanding of dispersal patterns in changing environments.

Desiccation stress can potentially act as both a cause and a cost of dispersal. A high desiccation stress may drive individuals away from an area, while at the same time, the process of movement can incur desiccation stress to the dispersers. Since males and females in sexually dimorphic species often differ in the amount of body resources and their partitioning along the survival-reproduction axis (Rantala and Roff 2007; Wilkin and Sheldon 2009; Maklakov and Lummaa 2013), differences in their desiccation profiles are commonplace (Jill and Daniel 2003; Matzkin et al. 2007; Lyons et al. 2014). Similarly, many species exhibit sex-biased dispersal, a possible reflection of asymmetric cost-benefit outcomes of dispersal between the sexes (Trochet et al. 2016; Li and Kokko 2019). While the relationships among environmental stress, dispersal, and sex have been recently discussed (Gerber and Kokko 2018), sex differences in the dispersal-desiccation relationship have typically not been studied. Given that investigations into sex differences in dispersal syndromes are relatively rare, this is hardly surprising (but see Legrand et al. 2016; Mishra et al. 2018a). The presence of pervasive sex differences in the life history and behavior literature leads us to anticipate some sex differences in the relationship between dispersal and desiccation stress as well. Especially in terms of dispersal costs, it would be interesting to see how the desiccation stress incurred during movement compares with other dispersal-related fitness costs, such as female fecundity (Roff and Fairbairn 2007; Guerra 2011).

Here we investigate the relationship between desiccation stress and dispersal, as well as the associated sex differences, using populations of *Drosophila melanogaster* under controlled environmental conditions. Interestingly, both a pos-

itive and a negative association of desiccation stress with dispersal has already been reported in *D. melanogaster* (Mishra et al. 2018a), thus making it a suitable system to delineate how the desiccation-dispersal relationship is shaped. Specifically, we asked the following questions: (1) Does desiccation stress act as a cause of dispersal in males and females? (2) Is desiccation stress a cost of dispersal in males and females? (3) Does dispersal evolution alter the desiccation cost of dispersal in either sex, and (4) Do females experience a fecundity cost of dispersal? Our results showed that desiccation stress acts as a significant cause for dispersal for both sexes. However, desiccation stress emerged as a cost of dispersal largely in the males and was not altered by dispersal evolution. Finally, while the females paid a negligible desiccation cost of dispersal, they experienced a significant cost of dispersal in terms of their fecundity. We discuss these results in the context of *Drosophila* physiology, along with their implications for dispersal patterns.

Methods

Fly Populations

We used large outbred laboratory populations (breeding size, ~2,400 individuals) of *Drosophila melanogaster* for all the experiments in this study. The ancestry of these populations can be traced back to the IV lines, which were wild-caught in South Amherst, Massachusetts (Ives 1970). The single-generation experiments in this study were conducted using a baseline population named DB₄ (Sah et al. 2013; Mishra et al. 2020b). In addition, we used four dispersal-selected populations (namely, VB₁₋₄) and their corresponding controls, the nonselected populations (VBC₁₋₄), for one experiment. Because of the ongoing selection for higher dispersal every generation, the VB populations have evolved a higher dispersal propensity and ability (Tung et al. 2018b), as well as lower desiccation resistance (Mishra et al. 2018a), compared with the VBC populations. All the populations were maintained in discrete-generation cycles under uniform environmental conditions of 25°C temperature, 80%–90% humidity, and 24-h light.

Dispersal Setup

Following previous studies (Mishra et al. 2018a; Tung et al. 2018b), we used a two-patch dispersal setup for observing fly dispersal. Each dispersal setup comprised a source container, a path tube, and a destination container (fig. 1). In this setup, all the flies for a given treatment/group are first introduced into the source container, which opens into a transparent plastic tube (internal diameter, ~1 cm) that serves as the path. The other end of the path tube leads into the destination container, thereby allowing the dispersal of flies from

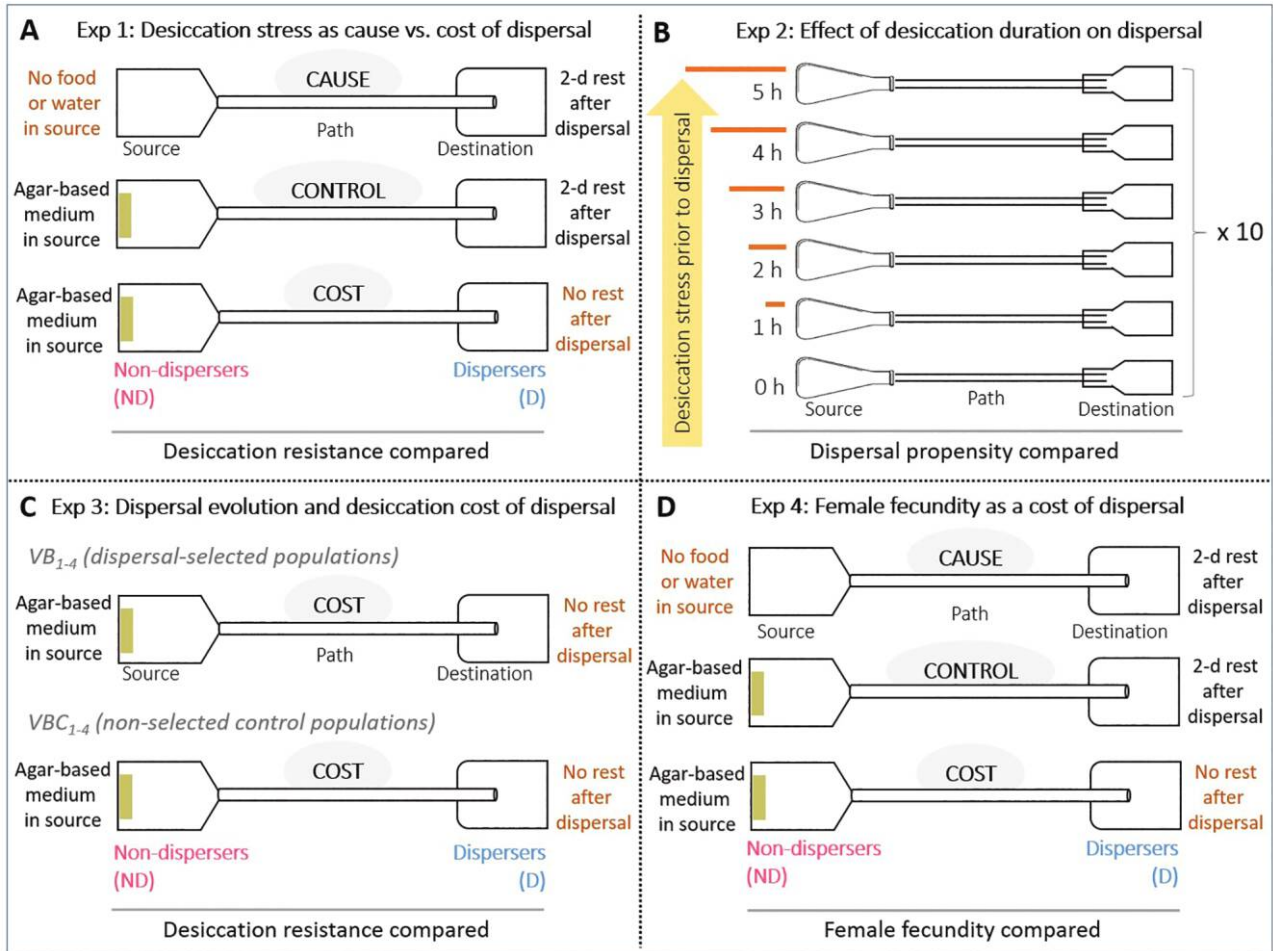


Figure 1: Schematics of the experimental design. **A**, Experiment 1 investigated the role of desiccation stress as a cause versus cost of dispersal. Using a source-path-destination setup, age-matched flies from an outbred baseline population (DB_4) were segregated into nondisperser (ND) populations and disperser (D) populations under three scenarios: cause (no food or water in source, rest provided after dispersal run), control (agar-based banana-jaggery medium in source, rest provided after dispersal run), and cost (agar-based banana-jaggery medium in source, no rest provided after dispersal run). ND and D flies in each scenario were then assayed for their desiccation resistance. **B**, Experiment 2 further examined the role of desiccation stress as a cause of dispersal. Groups of age-matched flies from the DB_4 population were subjected to different durations of desiccation stress (0–5 h) before being subjected to dispersal assay. **C**, Experiment 3 investigated whether the desiccation cost of dispersal differs between populations selected for higher dispersal (VB_{1-4}) and their nonselected controls (VBC_{1-4}). Desiccation resistance of all eight population blocks was compared under the cost scenario similar to experiment 1. **D**, Experiment 4 examined the role of female fecundity as a cause versus cost of dispersal. Here, female ND and D flies for the three scenarios (cause, control, and cost) were assayed for their fecundity.

the source to the destination container through the path for a fixed duration. The path protrudes into the destination container by a small length (~3 cm) to limit the backflow of flies from the destination (Mishra et al. 2018b). Depending on the experiment, the size of the source and destination containers, as well as the length of the path tube, can be customized. A single experiment typically involves multiple such dispersal setups maintained under uniform environmental conditions. At the end of a dispersal run, these dispersal setups are dismantled, and the flies found in each part (source/path/destination) are used as per the experimental requirements.

Experiments

We carried out a series of experiments to address various questions related to causes and costs of dispersal. The protocols, type of data obtained, and statistical analyses are presented separately below for each experiment.

Experiment 1: Desiccation Stress as Cause versus Cost of Dispersal. We first examined whether desiccation stress acts as a cause and emerges as a cost of dispersal in *D. melanogaster*. For this, we started with ~19,200 age-matched

adult flies (12 days old from egg collection) from the DB₄ population that were reared under identical conditions of ad lib. food and water. Cylindrical, translucent plastic containers (~1.5 L volume) were used as “source” and “destination,” along with a path length of 6 m, to assemble two-patch dispersal setups (as described in “Dispersal Setup”). Batches of the aforementioned DB₄ individuals were then introduced into eight such dispersal setups (~2,400 individuals per setup) and allowed to disperse for 5 h. By modulating two factors—that is, the presence of agar-based food (banana-jaggery medium) in the “source” container and the provision of rest (2 days with ad lib. food and water) to flies after the dispersal run—we devised three scenarios (fig. 1A): (a) the cause scenario, where we could identify whether desiccation stress was a cause of dispersal; (b) the control scenario, where desiccation stress was expected to be neither a cause nor a cost of dispersal; and (c) the cost scenario, where we could identify whether desiccation stress was a cost of dispersal. In each of the three scenarios, the flies that completed dispersal from the source to the destination were termed dispersers (D), whereas the flies found inside the source container were termed nondispersers (ND). The flies found in the path at the end of the dispersal run were not used in this experiment.

In the cause scenario, there was no food or water in the source, making desiccation stress a likely driver of dispersal away from the source. After the dispersal event, we collected the ND and D flies separately and provided them a 2-day rest with ad lib. food and water, so that the D flies could recuperate any energy costs of dispersal run (similar to Mishra et al. 2018a). Thereafter, we assayed 200 ND and 200 D flies (100 males + 100 females each) for their desiccation resistance (see “Assay Details”) to assess whether they differed in terms of their inherent desiccation sensitivity (fig. 1A, cause scenario).

In the control scenario, we provided agar-based banana-jaggery medium in the source container during the dispersal run, thereby removing desiccation stress as a possible driver of dispersal. Similar to the cause scenario, the dispersal event was followed by a 2-day rest for both ND and D flies, to offset any energy costs of dispersal (fig. 1A, control scenario). Subsequently, we compared the desiccation resistance of 200 ND and 200 D flies to ascertain whether there were any unaccounted for differences between them, that is, other than those detected in the cause and cost scenarios.

The cost scenario was complementary to the cause scenario. Here we provided banana-jaggery medium in the source container, thereby removing desiccation stress as a cause of dispersal, but did not allow any rest after dispersal. As described above, we then compared the desiccation resistance of 200 ND and 200 D flies, with any difference attributed to the energy costs of dispersal (fig. 1A, cost scenario).

In the cause scenario, the flies lacked both food and water, thus potentially conflating starvation with desiccation. However, *D. melanogaster* flies typically die of desiccation stress three to six times sooner than they die of starvation (van Herrewege and David 1997; Parkash and Munjal 2000; Matzkin et al. 2009). Thus, although the flies do experience starvation along with desiccation, it is reasonable to state that the latter is the primary cause of stress in this short duration.

The statistical analyses for this experiment, as well as those described in subsequent sections, were carried out in R ver. 4.0.3 (R Core Team 2020). Here the desiccation data from experiment 1 were analyzed together in a single mixed generalized linear model (GLM) using the lmer function from lme4 package ver. 1.1-25 (Bates et al. 2015), with scenario (cause/control/cost), dispersal (ND/D), and sex (male/female) as the fixed factors. As the flies were assayed in single-sex groups of 10 individuals within a vial (see “Assay Details”), we included vial identity (1–10) as a random factor that was nested within the scenario × dispersal × sex interaction. Following a type III analysis of deviance to ascertain the significance of the fixed factors and their interactions in GLM via the ANOVA function in car package ver. 3.0-10 (Fox and Weisberg 2019), we carried out the relevant pairwise comparisons using the pairs function in emmeans package ver. 1.5.2-1 (Lenth 2020). Cohen’s *d* was used as a measure of effect size for significantly different pairs of means, with the effect interpreted as large, medium, and small for $d \geq 0.8$, $0.8 > d \geq 0.5$, and $d < 0.5$, respectively (Cohen 1988).

Experiment 2: Effect of Desiccation Duration on Dispersal.

Here we investigated how dispersal changes with the duration of desiccation stress. For this, we segregated age-matched DB₄ flies (12 days old from egg collection) into multiple groups of 120 individuals (60 males + 60 females) that were subjected to varying durations of desiccation stress (0, 1, 2, 3, 4, and 5 h) before being subjected to dispersal assay in separate dispersal setups (fig. 1B). The source here was a 100-mL glass flask without any food or water, the path length was 2 m, and the destination was a 250-mL plastic bottle. The dispersal assay lasted 2 h. The path length and dispersal duration for experiment 2 were kept shorter than those in experiment 1, because unlike experiment 1, the flies here had already undergone some desiccation stress (i.e., 0–5 h) before the dispersal assay. Following a previous protocol (Mishra et al. 2018b, 2020a, 2020b), the experiment was carried out over 10 consecutive days with a fresh set of age-matched flies every day. This allowed us to assay one replicate of every desiccation treatment each day, yielding 10 replicates blocked by day. In total, 6,000 flies (5 desiccation treatments × 2 sexes × 10 days × 60 flies treatment⁻¹ sex⁻¹ day⁻¹) were assayed for this experiment. From the dispersal assay, we collected data on dispersal propensity (i.e., the fraction of flies that dispersed from

the source; see “Assay Details”). To account for any day-to-day microenvironmental variation, we used “day” as a random blocking factor in the analysis. Therefore, the dispersal propensity data were analyzed in a mixed model binomial GLM (with logit link function) using the `glmer` function from `lme4` package ver. 1.1-25 (Bates et al. 2015), with desiccation duration (0, 1, 2, 3, 4, and 5 h) and sex (male and female) as fixed factors and day (1–10) as the random factor. Following analysis of deviance via the ANOVA function in `car` package ver. 3.0-10 (Fox and Weisberg 2019), appropriate pairwise comparisons were carried out using the `pairs` function in `emmeans` package ver. 1.5.2-1 (Lenth 2020).

Experiment 3: Dispersal Evolution and Desiccation Cost of Dispersal. Here we used dispersal-selected populations (VB_{1-4}), which have a ~100% higher dispersal propensity, travel ~67% longer distances (Tung et al. 2018b), and exhibit a lower desiccation resistance (Mishra et al. 2018a) than their nonselected controls (VBC_{1-4}). In this experiment, we investigated whether the VB and VBC populations differ in their desiccation cost of dispersal. This would help determine whether selection for dispersal under desiccated conditions has altered the magnitude of proximate cost paid by dispersers. We subjected ~2,400 age-matched individuals per population block (1–4) of each population type (VB/VBC) to segregation into ND and D individuals under the cost scenario as described in experiment 1 (fig. 1C). Thereafter, we assayed 100 males and 100 females (in groups of 10 individuals per vial) from each of the eight populations (VB_{1-4} and VBC_{1-4}) for their desiccation resistance (see “Assay Details”). The entire desiccation resistance data were analyzed using a mixed model GLM with the `lmer` function in `lme4` package ver. 1.1-25 (Bates et al. 2015), with dispersal selection (VB/VBC), dispersal (ND/D) and sex (male/female) as fixed factors, and population block (1–4) and vial identity (1–10) as random factors. Here vial identity was nested inside the dispersal selection \times dispersal \times sex \times population block term. Following the GLM, we used the ANOVA function in `car` package ver. 3.0-10 (Fox and Weisberg 2019) for analysis of deviance and subsequently the `pairs` function in `emmeans` package ver. 1.5.2-1 (Lenth 2020) for relevant pairwise comparisons.

Experiment 4: Female Fecundity as Cause versus Cost of Dispersal. This experiment aimed to examine whether females paid a dispersal cost in terms of their fecundity. The female flies in this experiment were from the same ND and D groups of flies that were segregated in experiment 1, giving rise to (a) the cause scenario, defined by the lack of suitable oviposition site in source container (b); the control scenario, with suitable oviposition surface (i.e., banana-jaggery medium) in the source and provision of rest after dispersal run; and (c) the cost scenario, where no rest is provided and flies

were assayed for their fecundity immediately after dispersal (fig. 1D). We counted the female fecundity as the number of eggs laid over a 12-h period, with the ND and D flies for each scenario assayed together (see “Assay Details”). The entire fecundity data were analyzed together with a quasi-Poisson GLM (with log link function) using the `glm` function in `stats` package ver. 4.0.3 (R Core Team 2020), with scenario (cause, control, and cost) and dispersal (ND and D) as the fixed factors. As described above, we used the ANOVA function in `car` package ver. 3.0-10 (Fox and Weisberg 2019) for analysis of deviance and the `pairs` function in `emmeans` package ver. 1.5.2-1 (Lenth 2020) for relevant pairwise comparisons.

Assay Details

Desiccation Resistance Assay (Experiments 1 and 3). Desiccation resistance for a fly was measured as the duration that it could survive without food and moisture. To quantify this, same-sex groups of 10 flies each were introduced into empty, transparent (35 mL) vials and monitored until the death of the last fly in each vial, in a well-lit environment maintained at 25°C and between 80% and 90% humidity. The survivorship checks were conducted every 2 h, and 10 such replicate vials were used per sex.

Dispersal Assay (Experiment 2). For every two-patch dispersal setup (replicate), we counted the number of male and female flies that reached the destination until the end of the dispersal assay (2 h). In addition, we recorded the number and sex of flies that emigrated from the source but did not reach the destination, that is, those found within the path tube at the end of the dispersal assay. These data were used to estimate the dispersal propensity, that is, the proportion of flies that initiated dispersal from the source (Friedenberg 2003).

Fecundity Assay (Experiment 4). Female fecundity was assessed as the number of eggs laid per female over a 12-h period. The flies were anesthetized under mild CO₂, and pairs of one male and one female each were introduced into individual 50-mL centrifuge tubes containing a banana-jaggery food cup. The tube had provision for aeration, and the food cup provided a surface for laying eggs. Forty such replicates were set up per group (i.e., dispersers/nondispersers) per scenario. The setups were left undisturbed for 12 h in a well-lit environment maintained at 25°C and between 80% and 90% humidity. At the end of 12 h, the flies were discarded, and the eggs laid on the food were counted under a stereomicroscope.

Results

Desiccation Stress as Cause versus Cost of Dispersal

Desiccation resistance data from experiment 1 showed a significant scenario \times dispersal \times sex interaction ($\chi^2_2 = 7.20$,

$P = .027$). Analysis of pairwise differences for this interaction revealed a number of results (supplemental PDF, text S1.1). First, there was no difference in the desiccation resistance of dispersers versus nondispersers in the control scenario ($P_{\text{males}} = .16$, $P_{\text{females}} = .34$; fig. 2B, 2E). This was expected, as all these flies had access to ad lib. food and water in the source container, as well as a 2-day rest after the dispersal event. Second, dispersers in the cause scenario had a lower desiccation resistance than nondispersers ($P_{\text{males}} = .006$, $d = 1.63$, large; $P_{\text{females}} = .005$, $d = 1.10$, large; fig. 2A, 2D). This implies that desiccation stress likely served as a cause of dispersal in both sexes. Third, while males experienced a cost of dispersal in terms of their desiccation resistance ($P < 10^{-4}$, $d = 1.21$, large), no such cost was seen in females ($P = .86$; fig. 2C, 2F).

Desiccation Stress as a Cause of Dispersal in Both Sexes

The role of desiccation stress as a cause of dispersal was further investigated in experiment 2. Analysis of data from this experiment revealed that the desiccation duration \times sex interaction was significant ($\chi^2_5 = 17.10$, $P = .004$), indicating an asymmetric effect of desiccation duration

on dispersal propensity of males and females. However, pairwise comparisons revealed an increasing trend of dispersal propensity with longer durations of desiccation stress in both sexes, with a somewhat greater effect observed in males (fig. 3; supplemental PDF, text S1.2). Therefore, the results from both experiment 1 and experiment 2 suggested that desiccation stress served as a cause of dispersal in both sexes, with longer durations of desiccation leading to greater dispersal.

Desiccation Stress as a Sex-Biased Cost of Dispersal

Next, we examined the role of desiccation stress as a cost of dispersal using four dispersal-selected populations (VB_{1-4}) and their corresponding nonselected controls (VBC_{1-4} ; experiment 3). Desiccation resistance data from this experiment revealed a significant dispersal \times sex interaction ($\chi^2_1 = 9.52$, $P = .002$), with males experiencing a relatively larger desiccation cost of dispersal ($P < 10^{-4}$, $d = 1.86$, large; fig. 4A, 4B) than females ($P < 10^{-4}$, $d = 0.42$, small; fig. 4C, 4D). Moreover, the dispersal selection \times dispersal ($\chi^2_1 = 2.33$, $P = .13$) and dispersal selection \times dispersal \times sex ($\chi^2_1 = 0.19$, $P = .66$) interactions were not significant, indicating

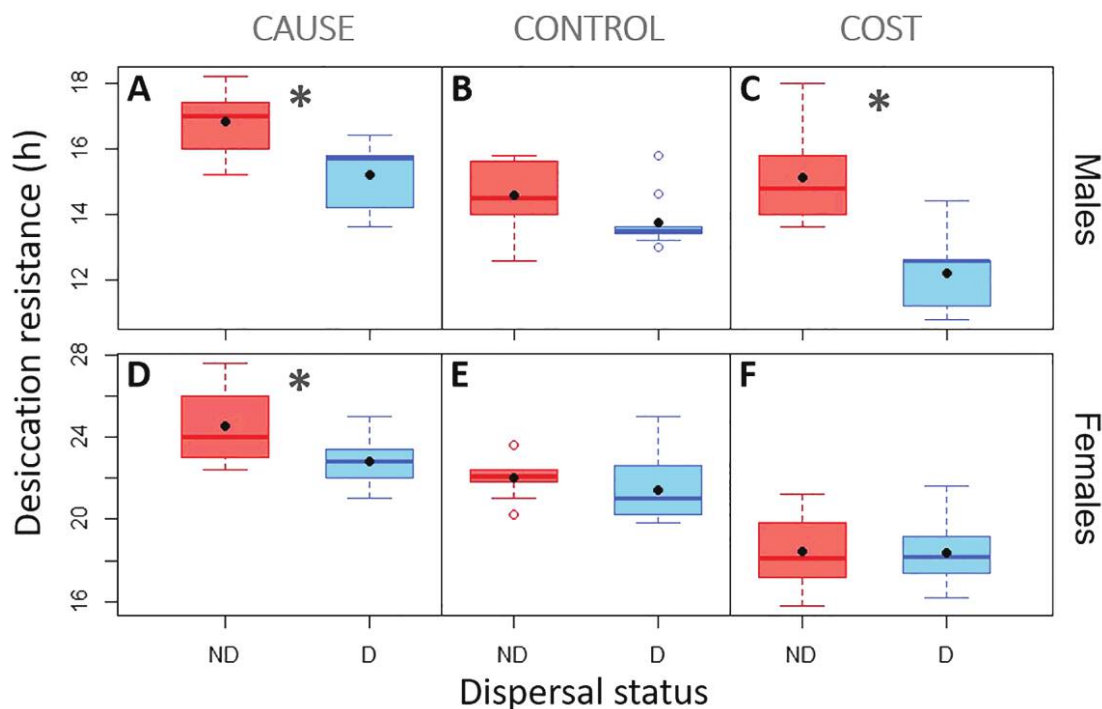


Figure 2: Desiccation stress as cause versus cost of dispersal (experiment 1). Desiccation resistance for nondisperser (ND) and disperser (D) flies from an outbred, baseline population (DB_i), under three scenarios: cause, control, and cost. Data for males and females are presented in the top and bottom rows, respectively. Edges of the boxplots represent 25th and 75th percentiles of the data. Circles represent means, and the lines inside the boxes represent medians. Asterisks indicate a significant difference ($P < .05$) between ND and D flies within a given panel. Note that the scales on the y-axis differ between the males and females. For exact P values, see the supplemental PDF, text S1.1.

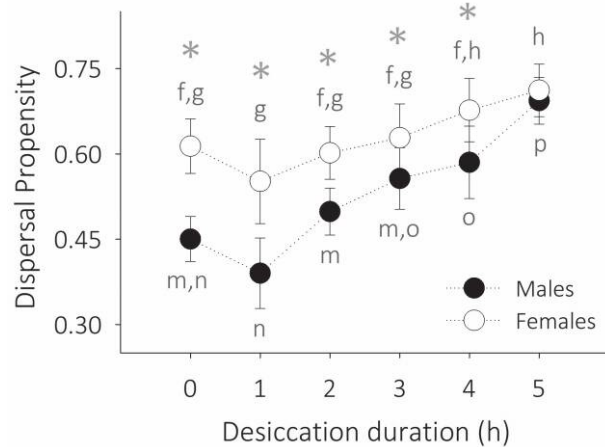


Figure 3: Effect of desiccation duration on dispersal propensity (Experiment 2). Dispersal propensity (\pm SE) for age-matched flies from an outbred baseline population (DB_4) subjected to desiccation stress for different durations (0–5 h). Each point represents the average of 10 replicates (each with 120 individuals). For a given sex, the changes in dispersal are examined by comparing the propensity means across the six desiccation durations (significant differences denoted using different lowercase letters—starting with “m” for males and “f” for females). Asterisks denote a significant difference in male and female dispersal for a given desiccation duration. For exact P values, see the supplemental PDF, text S1.2.

that this result was consistent for both control (VBC) and dispersal-selected (VB) populations (supplemental PDF, text S1.3).

Significant Cost of Dispersal for Females in Terms of Fecundity

As minimal or no desiccation cost of dispersal was observed for females in experiments 1 and 3, we investigated whether there was a reproductive cost of dispersal for the females (experiment 4). Analysis of the female fecundity data from this experiment (presented in the supplemental PDF, text S1.4) revealed a significant scenario \times dispersal interaction ($\chi^2_2 = 17.90$, $P = .0001$). Pairwise comparisons for this interaction revealed no significant difference between dispersers and nondispersers under the control scenario ($P = .63$; fig. 5B) and the cause scenario ($P = .16$; fig. 5A) but a significant difference in the cost scenario: disperser females had a lower fecundity than nondisperser females ($P = .0001$, $d = 0.68$, medium; fig. 5C). Therefore, we concluded that female flies pay a cost of dispersal in terms of their fecundity.

Discussion

Desiccation Stress as a Cause of Dispersal in Both Sexes

Environmental stress, among other things, can serve as a major cause of biological dispersal. At the same time, the

process of dispersal can be stressful to individuals. When monitored after a dispersal event, the stress-resistance ability of organisms is often found to be lower (Graves et al. 1992). This decrease can come about in three different ways. First, the dispersers might be the ones that were more susceptible to the stress, and hence they dispersed. Second, even if the stress resistance of the dispersers is inherently similar to that of the nondispersers, the energy spent in the act of dispersal reduces the stress-resistance ability of the former. Third, it might be an interaction of these two scenarios. Unfortunately, these questions are very difficult to answer, particularly when there is no a priori way of distinguishing between a disperser and a nondisperser. Here we investigated this complex relationship using desiccation as the type of stress and *Drosophila melanogaster* as a model system. Our experimental design allowed us to explicitly control for other confounds when a particular aspect of the desiccation-dispersal relationship was being examined.

To begin with, experiment 1 revealed that the disperser (D) flies had a lower desiccation resistance than the nondisperser (ND) flies under the cause scenario (fig. 2A, 2D). Comparing the results with the control scenario, which showed no difference between ND and D flies (fig. 2B, 2E), we could conclude that desiccation stress indeed served as a significant driver of dispersal for both male and female flies. This is in line with the expectation from the literature that dispersal is one of the foremost ways for escaping unfavorable conditions (Gerber and Kokko 2018), not only in animal taxa (Cremer and Heinze 2003; Riotte-Lambert and Matthiopoulos 2020) but also in plants (Martorell and Martínez-López 2014). While this is not a surprising result, our study demonstrates it explicitly using a unique setup, where we were able default to control for the possible confound of desiccation as a cost of dispersal (fig. 1A).

Going a step further, we demonstrate in experiment 2 how *Drosophila* dispersal changes with increasing desiccation stress (fig. 3). Given that desiccation resistance can be correlated with glycogen content in flies (Gibbs et al. 1997; although see Hoffmann and Harshman 1999), one might have expected a decrease in dispersal at longer desiccation durations, where the flies likely faced a severe depletion of their glycogen reserves (Folk and Bradley 2004; Bazinet et al. 2010). Surprisingly, however, this was not the case in experiment 2, where flies of both sexes showed a nearly monotonic increase in their dispersal propensity with increasing desiccation stress (fig. 3). This means that, at least for the duration of desiccation stress (up to 5 h) imposed in experiment 2, the flies were in a state to successfully initiate dispersal. However, as a corollary, it also means that organisms likely do not disperse until the stress turns acute, which may make them more susceptible to dispersal-related risks and costs (see “Sex-Biased Cost of Dispersal in Terms of Desiccation Stress”). It is possible that this delay in emigration could be a function of how long it

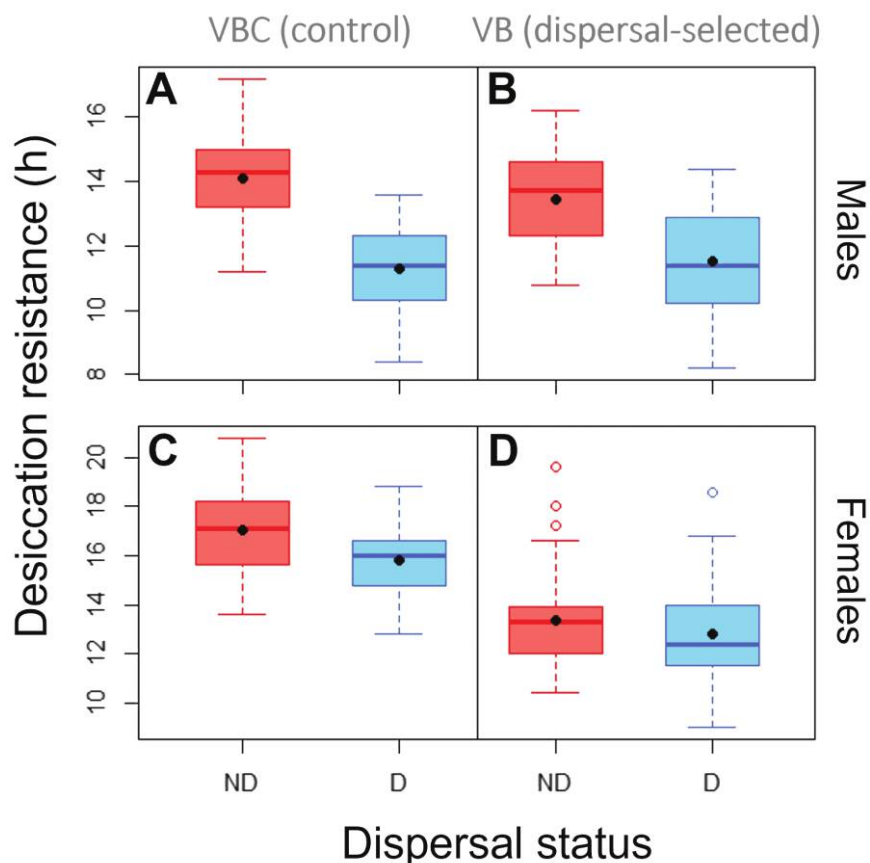


Figure 4: Dispersal evolution and desiccation cost of dispersal (experiment 3). Desiccation resistance of nondispersers (ND) and dispersers (D) from VB_{1-4} (dispersal-selected) populations and VBC_{1-4} (control) populations. Panels represent comparison between ND and D flies for VBC males (A), VB males (B), VBC females (C), and VB females (D). Edges of the boxplots represent 25th and 75th percentiles of the data. For the exact P values, see the supplemental PDF, text S1.3.

takes to initiate the stress physiological response. Since the cuticle of adult females (but not males) in *D. melanogaster* is known to undergo rapid desiccation hardening (RDH) in response to even short periods of desiccation exposure (Bazin et al. 2010; Stinziano et al. 2015), this could explain why males had a starker increase in dispersal than females (fig. 3). Overall, we speculate that the ability to perceive and react to stress would play a role in shaping the dispersal-mediated escape response from stressful habitats.

Since dispersal is also known to incur various costs (reviewed in Bonte et al. 2012), the process of dispersal itself can induce stress or increase the susceptibility of dispersing individuals to stress. We explored the potential desiccation cost of dispersal using the cost scenario in experiments 1 and 3.

Sex-Biased Cost of Dispersal in Terms of Desiccation Stress

Given that active dispersal involves expenditure of energy, it is likely that flies spend a part of their glycogen reserves

during dispersal (Graves et al. 1992), which can reduce their desiccation resistance following a dispersal event. Experiment 1 confirmed a cost of dispersal in terms of their desiccation resistance, although it was not symmetric between the two sexes. A significant desiccation cost of dispersal was observed for males (fig. 2C) but not for females (fig. 2F) in the DB_4 population. Similarly, experiment 3 revealed that the desiccation cost of dispersal was much higher in males (fig. 4A, 4B) than in females (fig. 4C, 4D; for the exact effect sizes, see “Results”). As both dispersal-selected flies (VB) and nonselected control flies (VBC) showed a male-biased desiccation cost, we concluded that the evolution of dispersal did not alter the immediate desiccation cost of dispersal between these populations.

A potential explanation for the sex bias in desiccation cost is the well-known sexual dimorphism in desiccation resistance of *D. melanogaster* adults: female flies tend to have a higher desiccation resistance than their male counterparts (Gibbs et al. 1997; Matzkin et al. 2007; Mishra et al. 2018a). As a result, the females likely had greater body

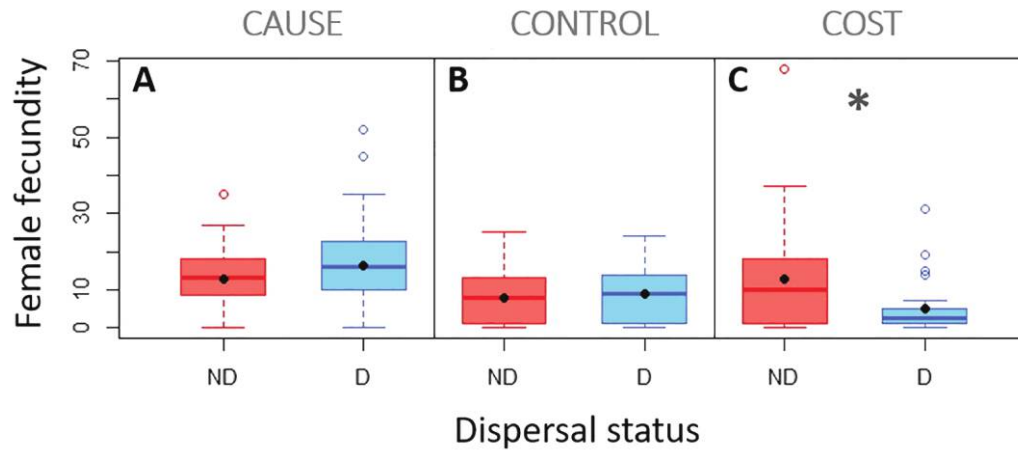


Figure 5: Female fecundity as cause versus cost of dispersal (experiment 4). Female fecundity for nondisperser (ND) and disperser (D) flies from an outbred, baseline population (DB_0), under three scenarios: cause, control, and cost. Edges of the boxplots represent 25th and 75th percentiles of the data. Asterisks indicate a significant difference ($P < .05$) between ND and D flies within a given panel. For the exact P values, see the supplemental PDF, text S1.4.

resources to begin with, which allowed them to successfully undertake dispersal without paying a high desiccation cost. This is also congruent with the observation that dispersal evolution has not led to a change in the body size of VB females relative to their VBC controls (Mishra et al. 2018a; Tung et al. 2018a). Another potential explanation here could be the RDH response seen exclusively in female flies, which reduces their rate of surface water loss via altered cuticular hydrocarbon composition (Bazinet et al. 2010; Stinziano et al. 2015).

It is possible that the dispersal cost for females manifests not in terms of their somatic maintenance (here, desiccation resistance) but rather in their reproductive output. This is in line with the results of several life history studies of trade-offs that show a reproductive cost instead of somatic costs in females (Miyatake 1997; Ghalambor and Martin 2001; Djawdan et al. 2004; Muller-Landau 2010). Given the energy-intensive nature of active dispersal (as evidenced by the dispersal cost borne by males in this study), it was possible that female fecundity could suffer as a cost of dispersal. Therefore, we next investigated this possibility.

Fecundity Cost of Dispersal for Female Flies

The relationship between dispersal and fecundity varies across taxa. A negative association between dispersal and fecundity has been reported in several wing-dimorphic insects (reviewed in Guerra 2011) and wing-monomorphic insects (reviewed in Tigreros and Davidowitz 2019), as well as in other taxa, such as *Caenorhabditis elegans* (Friedenberg 2003). These results are typically explained as a developmental or energetic

cost of dispersal in terms of fecundity. In contrast, a positive association between dispersal and fecundity has also been documented in many other insect taxa (Dingle et al. 1988; Rankin and Burchsted 1992; Hanski et al. 2006). Here the typical explanation is twofold. First, individuals with better body condition, including higher fecundity, could be better able to complete dispersal. Second, high fecundity could lead to high dispersal via increased kin competition in a given habitat. Of course, it is also possible that the dispersal-fecundity relationship, like other dispersal-trait associations, is modulated by the environmental context (e.g., Legrand et al. 2016; Mishra et al. 2018a). For instance, the fecundity cost of dispersal may be particularly strong under limiting resources. Similarly, the positive association between dispersal and fecundity might be altered by the population density and level of resources in the originating patch (e.g., Einum et al. 2006). Therefore, experiments under controlled conditions, which can take ecological context into account, can provide important insights into the relationship between fecundity and dispersal.

Experiment 4 revealed that while there was no difference under the cause and control scenarios, D females had a significantly lower fecundity than ND flies in the cost scenario (fig. 5). What makes our result interesting is that females showed a fecundity cost before the somatic cost of dispersal, at least in terms of desiccation resistance (cf. figs. 2F, 5C). A plausible explanation for this is that, under stressful conditions, individuals may prioritize survival over potential reproduction. This has been observed in other life history traits as well, where allocation of resources into somatic maintenance can, at times, take priority over reproductive investment

(Djawdan et al. 2004; Muller-Landau 2010; Martorell and Martínez-López 2014). In particular, given that dispersal is a key life history trait (Bonte and Doherty 2017) with several potential costs (Bonte et al. 2012), the fecundity trade-off observed here is in line with the observations for other wing-monomorphic insects (Tigreros and Davidowitz 2019).

Implications

Our results revealed desiccation as a cause of dispersal for both sexes in *D. melanogaster* and that dispersal propensity of both male and female flies increased with increasing desiccation duration. In addition, we observed a male-biased cost of dispersal in terms of desiccation resistance, while the female flies paid a fecundity cost of dispersal. We discuss some implications of our results below.

First, these results demonstrate that the relationship between stress and dispersal is likely complicated. On the one hand, stress is likely to drive dispersal of individuals away from an area. On the other hand, dispersing individuals incur a further cost of dispersal in terms of increased stress. Therefore, early dispersers from a population may be the least stress-tolerant individuals. In contrast, highly stress-tolerant individuals could delay emigration in response to a stress. These results are in line with a physiological threshold model of movement decision-making at the individual level (Goossens et al. 2020), which can translate to population-level effects. For instance, if dispersal occurs across habitats with high connectivity, stress-intolerant individuals may have the highest dispersal propensity (e.g., fig. 3). However, if the interhabitat connectivity is poor, only the relatively stress-resistant individuals in a population would be able to undertake dispersal successfully by surviving the large dispersal costs, representing an example of phenotypic ecological filtering (Renault et al. 2018). This can also translate to lower overall dispersal rates, potentially leading to instances of dispersal reduction (Waters et al. 2020).

Second, sex differences in the somatic costs of dispersal may effectively lead to instances of sex-biased dispersal, even if a similar number of male and female individuals emigrate from a given area. This is because the stress-sensitive sex (e.g., males in the current study) may not be able to complete dispersal as successfully as the stress-resistant sex (here, females). As a result, in the species where mating occurs after a dispersal event, such differences can lead to a skew in the local sex ratio of the dispersed population and consequently mate limitation. Moreover, the sex-biased nature of dispersal costs can result in demographic consequences through dispersal syndromes (Mishra et al. 2018a; Shaw et al. 2018). For instance, if the fecundity of immigrant females in a new area is reduced as a consequence of dispersal, then they may not be able to compete with the resident females in that area. As a result, the apparent prioritization of fitness cost over somatic cost

in females, as observed here, can hamper their settlement ability in a new habitat.

In this study, we used controlled laboratory settings, well-documented populations, and appropriate controls to investigate the association between two key life history traits, that is, dispersal and desiccation resistance. Since both of these traits are important for the fitness of natural populations, it is reasonable to ask how our results would map to such populations. Unfortunately, it is difficult to directly extrapolate our results to natural populations. This is because wild insect populations (including *Drosophila*) also experience passive dispersal through factors like wind and other animals (Dobzhansky 1973; Dickinson 2014; Leitch et al. 2021). Evidently, it becomes extremely complicated to study dispersal syndromes in the presence of such mixed strategies. Hence, we decided to focus purely on active ambulatory dispersal, which precludes a comparison of our results with cases of mixed dispersal in nature. Moreover, in situ investigation of life history traits like desiccation resistance and fecundity are extremely difficult, which often requires such studies to happen in freshly caught populations in the laboratory (e.g., Parkash and Munjal 2000; Matzkin et al. 2009). However, it is known that a change in environment can alter the observed trait associations (Service and Rose 1985), which are expected to take considerable time for stabilization (Sgrò and Partridge 2000). This implies that studies investigating such associations are best performed in populations that have adapted for a long time to a relatively stable environment. Since natural populations mostly experience fluctuating environmental conditions, trait associations in such populations are expected to be much noisier, again precluding a direct comparison with our results. Thus, the primary strength of our microcosm study is the fact that these confounding factors could be adequately controlled, such that the relationship between desiccation resistance and dispersal could be appropriately investigated.

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Statement of Authorship

A.M. and S.D. conceived the ideas and designed the methodology; A.M., S.T., V.R.S.S., and P.M.S. collected the data, which A.M. analyzed; and A.M. and S.D. led the writing of the manuscript. All authors contributed critically to the manuscript and gave their final approval for publication.

Data and Code Availability

The data for this article are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.83bk3j9sq>; Mishra et al. 2022).

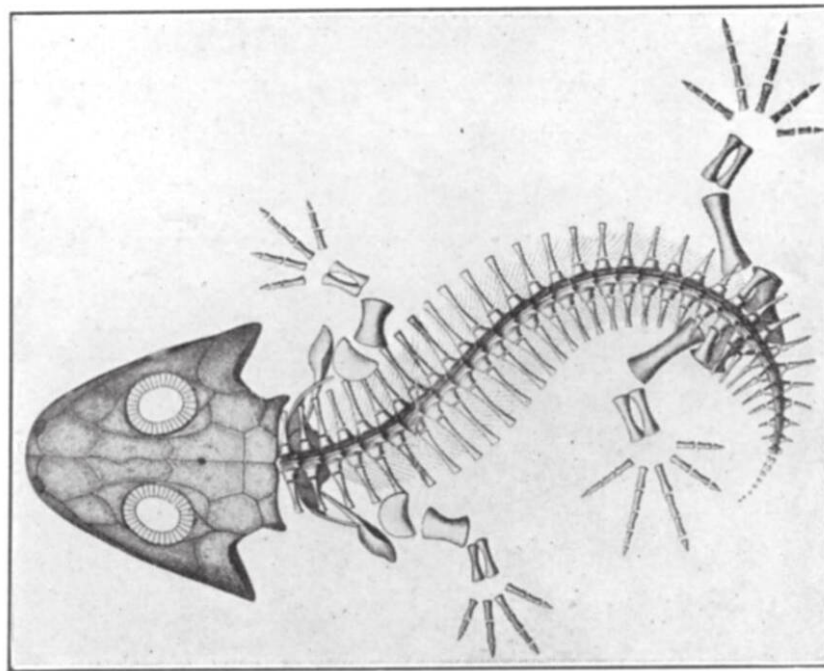
Literature Cited

- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bazinnet, A. L., K. E. Marshall, H. A. MacMillan, C. M. Williams, and B. J. Sinclair. 2010. Rapid changes in desiccation resistance in *Drosophila melanogaster* are facilitated by changes in cuticular permeability. *Journal of Insect Physiology* 56:2006–2012.
- Black, M., and H. W. Pritchard. 2002. Desiccation and survival in plants: drying without dying. Cabi, New York.
- Bonte, D., and M. Doherty. 2017. Dispersal: a central and independent trait in life history. *Oikos* 126:472–479.
- Bonte, D., H. Van Dyck, J. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehoucq, et al. 2012. Costs of dispersal. *Biological Reviews* 87:290–312.
- Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80:205–225.
- Chippindale, A. K., A. L. Ngo, and M. R. Rose. 2003. The devil in the details of life-history evolution: instability and reversal of genetic correlations during selection on *Drosophila* development. *Journal of Genetics* 82:133–145.
- Cohen, J. 1988. *Statistical power analysis for the behavioral sciences*. Erlbaum, Mahwah, NJ.
- Comte, L., and J. Olden. 2018. Evidence for dispersal syndromes in freshwater fishes. *Proceedings of the Royal Society B* 285:20172214.
- Cremer, S., and J. Heinze. 2003. Stress grows wings: environmental induction of winged dispersal males in *Cardiocondyla* ants. *Current Biology* 13:219–223.
- Dickinson, M. H. 2014. Death Valley, *Drosophila*, and the Devonian toolkit. *Annual Review of Entomology* 59:51–72.
- Dingle, H. 1974. The experimental analysis of migration and life-history strategies in insects. Pages 329–342 in L. B. Browne, ed. *Experimental analysis of insect behaviour*. Springer, Berlin.
- Dingle, H., K. E. Evans, and J. O. Palmer. 1988. Responses to selection among life-history traits in a nonmigratory population of milkweed bugs (*Oncopeltus fasciatus*). *Evolution* 42:79–92.
- Djawdan, M., T. T. Sugiyama, L. K. Schlaeger, T. J. Bradley, and M. R. Rose. 2004. Metabolic aspects of the trade-off between fecundity and longevity in *Drosophila melanogaster*. Pages 145–164 in M. R. Rose, M. Matos, and H. B. Passananti, eds. *Methuselah flies: a case study in the evolution of aging*. World Scientific, London.
- Dobzhansky, T. 1973. Active dispersal and passive transport in *Drosophila*. *Evolution* 27:565–575.
- Einum, S., L. Sundt-Hansen, and K. H. Nislow. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* 113:489–496.
- Folk, D. G., and T. J. Bradley. 2004. The evolution of recovery from desiccation stress in laboratory-selected populations of *Drosophila melanogaster*. *Journal of Experimental Biology* 207:2671–2678.
- Fox, J., and S. Weisberg. 2019. *An R companion to applied regression*. 3rd ed. Sage, Thousand Oaks, CA. <https://socialsciences.mcmaster.ca/jfox/books/companion/>.
- Friedenberg, N. A. 2003. Experimental evolution of dispersal in spatiotemporally variable microcosms. *Ecology Letters* 6:953–959.
- Gerber, N., and H. Kokko. 2018. Abandoning the ship using sex, dispersal or dormancy: multiple escape routes from challenging conditions. *Philosophical Transactions of the Royal Society B* 373:20170424.
- Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science* 292:494–497.
- Gibbs, A. G., A. K. Chippindale, and M. R. Rose. 1997. Physiological mechanisms of evolved desiccation resistance in *Drosophila melanogaster*. *Journal of Experimental Biology* 200:1821–1832.
- Goossens, S., N. Wybouw, T. Van Leeuwen, and D. Bonte. 2020. The physiology of movement. *Movement Ecology* 8:1–13.
- Graves, J. L., E. C. Toolson, C. Jeong, L. N. Vu, and M. R. Rose. 1992. Desiccation, flight, glycogen, and postponed senescence in *Drosophila melanogaster*. *Physiological Zoology* 65:268–286.
- Gros, A., T. Hovestadt, and H. J. Poethke. 2008. Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. *Ecological Modelling* 219:226–233.
- Guerra, P. 2011. Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. *Biological Reviews* 86:813–835.
- Hanski, I., M. Saastamoinen, and O. Ovaskainen. 2006. Dispersal-related life-history trade-offs in a butterfly metapopulation. *Journal of Animal Ecology* 75:91–100.
- Hoffmann, A. A., R. J. Hallas, J. A. Dean, and M. Schiffer. 2003. Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science* 301:100–102.
- Hoffmann, A. A., and L. G. Harshman. 1999. Desiccation and starvation resistance in *Drosophila*: patterns of variation at the species, population and intrapopulation levels. *Heredity* 83:637–643.
- Holmström, M., K. Hedlund, and H. Boriss. 2002. Drought acclimation and lipid composition in *Folsomia candida*: implications for cold shock, heat shock and acute desiccation stress. *Journal of Insect Physiology* 48:961–970.
- Holzinger, A., and U. Karsten. 2013. Desiccation stress and tolerance in green algae: consequences for ultrastructure, physiological and molecular mechanisms. *Frontiers in Plant Science* 4:327.
- Ives, P. T. 1970. Further genetic studies of the South Amherst population of *Drosophila melanogaster*. *Evolution* 24:507–518.
- Jessup, C., and B. Bohannan. 2008. The shape of an ecological trade-off varies with environment. *Ecology Letters* 11:947–959.
- Jill, D., and R. F. Daniel. 2003. The effects of size, sex, and reproductive condition on thermal and desiccation stress in a riparian spider (*Pirata sedentarius*, Araneae, Lycosidae). *Journal of Arachnology* 31:278–284.
- Karan, D., and R. Parkash. 1998. Desiccation tolerance and starvation resistance exhibit opposite latitudinal clines in Indian geographical populations of *Drosophila kikkawai*. *Ecological Entomology* 23:391–396.

- Kellermann, V., B. Van Heerwaarden, C. M. Sgrò, and A. A. Hoffmann. 2009. Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science* 325:1244–1246.
- Kranner, I., R. Beckett, A. Hochman, and T. H. Nash Iii. 2008. Desiccation-tolerance in lichens: a review. *Bryologist* 111:576–593.
- Legrand, D., N. Larranaga, R. Bertrand, S. Ducatez, O. Calvez, V. M. Stevens, and M. Baguette. 2016. Evolution of a butterfly dispersal syndrome. *Proceedings of the Royal Society B* 283:20161533.
- Legrand, D., A. Trochet, S. Moulherat, O. Calvez, V. M. Stevens, S. Ducatez, J. Clobert, et al. 2015. Ranking the ecological causes of dispersal in a butterfly. *Ecography* 38:822–831.
- Leitch, K. J., F. V. Ponce, W. B. Dickson, F. van Breugel, and M. H. Dickinson. 2021. The long-distance flight behavior of *Drosophila* supports an agent-based model for wind-assisted dispersal in insects. *Proceedings of the National Academy of Sciences of the USA* 118:e2013342118.
- Lenth, R. 2020. emmeans: estimated marginal means, aka least-squares means. R package version 1.5.2-1. R Foundation for Statistical Computing, Vienna. <https://cran.r-project.org/package=emmeans>.
- Li, X. Y., and H. Kokko. 2019. Sex-biased dispersal: a review of the theory. *Biological Reviews* 94:721–736.
- Lyons, C. L., M. Coetzee, J. S. Terblanche, and S. L. Chown. 2014. Desiccation tolerance as a function of age, sex, humidity and temperature in adults of the African malaria vectors *Anopheles arabiensis* and *Anopheles funestus*. *Journal of Experimental Biology* 217:3823–3833.
- Maklakov, A. A., and V. Lummaa. 2013. Evolution of sex differences in lifespan and aging: causes and constraints. *BioEssays* 35:717–724.
- Martorell, C., and M. Martínez-López. 2014. Informed dispersal in plants: *Heterosperma pinnatum* (Asteraceae) adjusts its dispersal mode to escape from competition and water stress. *Oikos* 123:225–231.
- Matthysen, E. 2012. Multicausality of dispersal: a review. Pages 3–18 in J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock, eds. *Dispersal ecology and evolution*. Oxford University Press, Oxford.
- Matzkin, L., T. D. Watts, and T. A. Markow. 2007. Desiccation resistance in four *Drosophila* species: sex and population effects. *Fly* 1:268–273.
- Matzkin, L. M., T. D. Watts, and T. A. Markow. 2009. Evolution of stress resistance in *Drosophila*: interspecific variation in tolerance to desiccation and starvation. *Functional Ecology* 23:521–527.
- Mishra, A., P. P. Chakraborty, and S. Dey. 2020a. Dispersal evolution diminishes the negative density dependence in dispersal. *Evolution* 74:2149–2157.
- Mishra, A., S. Tung, P. M. Shreenidhi, M. A. Sadiq, V. R. S. Sruti, P. P. Chakraborty, and S. Dey. 2018a. Sex differences in dispersal syndrome are modulated by environment and evolution. *Philosophical Transactions of the Royal Society B* 373:20170428.
- Mishra, A., S. Tung, V. R. S. Sruti, P. M. Shreenidhi, and S. Dey. 2022. Data from: Desiccation stress acts as cause as well as cost of dispersal in *Drosophila melanogaster*. *American Naturalist*, Dryad Digital Repository, <https://doi.org/10.5061/dryad.83bk3j9sq>.
- Mishra, A., S. Tung, V. R. S. Sruti, M. A. Sadiq, S. Srivathsa, and S. Dey. 2018b. Pre-dispersal context and presence of opposite sex modulate density dependence and sex bias of dispersal. *Oikos* 127:1596–1604.
- Mishra, A., S. Tung, V. R. S. Sruti, S. Srivathsa, and S. Dey. 2020b. Mate-finding dispersal reduces local mate limitation and sex bias in dispersal. *Journal of Animal Ecology* 89:2089–2098.
- Miyatake, T. 1997. Genetic trade-off between early fecundity and longevity in *Bactrocera cucurbitae* (Diptera: Tephritidae). *Heredity* 78:93–100.
- Muller-Landau, H. C. 2010. The tolerance-fecundity trade-off and the maintenance of diversity in seed size. *Proceedings of the National Academy of Sciences of the USA* 107:4242–4247.
- Parkash, R., and A. K. Munjal. 2000. Evidence of independent climatic selection for desiccation and starvation tolerance in Indian tropical populations of *Drosophila melanogaster*. *Evolutionary Ecology Research* 2:685–699.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.r-project.org>.
- Rajpurohit, S., O. Nedved, and A. G. Gibbs. 2013. Meta-analysis of geographical clines in desiccation tolerance of Indian drosophilids. *Comparative Biochemistry and Physiology A* 164:391–398.
- Rankin, M. A., and J. C. A. Burchsted. 1992. The cost of migration in insects. *Annual Review of Entomology* 37:533–559.
- Rantala, M. J., and D. A. Roff. 2007. Inbreeding and extreme outbreeding cause sex differences in immune defence and life history traits in *Epirrita autumnata*. *Heredity* 98:329–336.
- Renault, D., M. Laparie, S. J. McCauley, and D. Bonte. 2018. Environmental adaptations, ecological filtering, and dispersal central to insect invasions. *Annual Review of Entomology* 63:345–368.
- Riotte-Lambert, L., and J. Matthiopoulos. 2020. Environmental predictability as a cause and consequence of animal movement. *Trends in Ecology and Evolution* 35:163–174.
- Roff, D. A. 1977. Dispersal in dipterans: its costs and consequences. *Journal of Animal Ecology* 46:443–456.
- Roff, D. A., and D. J. Fairbairn. 2007. The evolution and genetics of migration in insects. *BioScience* 57:155–164.
- Ronce, O., and J. Clobert. 2012. Dispersal syndromes Pages 119–138 in J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock, eds. *Dispersal ecology and evolution*. Oxford University Press, Oxford.
- Sah, P., J. P. Salve, and S. Dey. 2013. Stabilizing biological populations and metapopulations through adaptive limiter control. *Journal of Theoretical Biology* 320:113–123.
- Service, P. M., and M. R. Rose. 1985. Genetic covariation among life-history components: the effect of novel environments. *Evolution* 39:943–945.
- Sgrò, C. M., and L. Partridge. 2000. Evolutionary responses of the life history of wild-caught *Drosophila melanogaster* to two standard methods of laboratory culture. *American Naturalist* 156:341–353.
- Shaw, A. K., H. Kokko, and M. G. Neubert. 2018. Sex difference and Allee effects shape the dynamics of sex-structured invasions. *Journal of Animal Ecology* 87:36–46.
- Stevens, V., S. Whitmee, L. Galliard, J. Clobert, K. Böhning-Gaese, D. Bonte, M. Brändle, et al. 2014. A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecology Letters* 17:1039–1052.
- Stinziano, J. R., R. J. Sové, H. D. Rundle, and B. J. Sinclair. 2015. Rapid desiccation hardening changes the cuticular hydrocarbon profile of *Drosophila melanogaster*. *Comparative Biochemistry and Physiology A* 180:38–42.
- Tigreros, N., and G. Davidowitz. 2019. Flight-fecundity trade-offs in wing-monomorphic insects. *Advances in Insect Physiology* 56:1–41.
- Trochet, A., E. A. Courtois, V. M. Stevens, M. Baguette, A. Chaîne, D. S. Schmeller, J. Clobert, et al. 2016. Evolution of sex-biased dispersal. *Quarterly Review of Biology* 91:297–320.

- Tuba, Z., N. G. Slack, and L. R. Stark. 2011. Bryophyte ecology and climate change. Cambridge University Press, Cambridge.
- Tung, S., A. Mishra, N. Gogna, M. A. Sadiq, P. M. Shreenidhi, V. R. S. Sruti, K. Dorai, et al. 2018a. Evolution of dispersal syndrome and its corresponding metabolomic changes. *Evolution* 72:1890–1903.
- Tung, S., A. Mishra, P. M. Shreenidhi, M. A. Sadiq, S. Joshi, V. R. S. Sruti, and S. Dey. 2018b. Simultaneous evolution of multiple dispersal components and kernel. *Oikos* 127:34–44.
- Van Heerwaarden, B., and C. M. Sgrò. 2014. Is adaptation to climate change really constrained in niche specialists? *Proceedings of the Royal Society B* 281:20140396.
- van Herrewege, J., and J. R. David. 1997. Starvation and desiccation tolerances in *Drosophila*: comparison of species from different climatic origins. *Ecoscience* 4:151–157.
- Wang, Y., J.-F. Ferveur, and B. Moussian. 2021. Eco-genetics of desiccation resistance in *Drosophila*. *Biological Reviews* 96:1421–1440.
- Waters, J. M., B. C. Emerson, P. Arribas, and G. A. McCulloch. 2020. Dispersal reduction: causes, genomic mechanisms, and evolutionary consequences. *Trends in Ecology and Evolution* 35:512–522.
- Wilkin, T. A., and B. C. Sheldon. 2009. Sex differences in the persistence of natal environmental effects on life histories. *Current Biology* 19:1998–2002.

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“Restoration of *Melanerpeton* from the Permian of Saxony. After Credner.” From “The Ancestry of the Caudate Amphibia” by Roy L. Moodie (*The American Naturalist*, 1908, 42:361–373).