Title: Evolution of dispersal kernel in laboratory populations of *Drosophila melanogaster*

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Abstract:

The distribution of dispersal distances in a population (i.e. the dispersal kernel) is often considered to be a non-evolvable property of a species. We tested this widely-held belief by subjecting four laboratory populations of *Drosophila melanogaster* to selection for increased dispersal. The dispersal kernel evolved rapidly, both in terms of the location parameter (i.e. mean distance travelled), as well as the shape parameters (e.g. skew and kurtosis). Consequently, the frequency of long-distance dispersers in the population increased, which enhanced the spatial extent of the selected populations by 67%. The selected populations also had significantly greater dispersal propensity and rate. The evolvability of dispersal kernels can potentially affect range expansion, invasion speed and disease spread, which in turn might have considerable socio-economic consequences.

1. Introduction

Dispersal, defined as movement of organisms or propagules leading to gene flow across space (Ronce 2007), influences several ecological processes including dynamics of local and metapopulations (Hanski 1999; Hanski and Gaggiotti 2004), life-history (Buoro and Carlson 2014; Stevens et al. 2013), invasion (Shaw and Kokko 2015), evolution of cooperation and sociality (Galliard et al. 2005) and community dynamics (Leibold et al. 2004). Since dispersal increases the probability of survival of individuals by allowing them to track the favorable environmental conditions, it is thought to be one of the primary mechanisms by which organisms are expected to cope with climate change (Travis et al. 2013). Yet there is considerable controversy in the literature on whether dispersal is an evolvable trait or not (Lowe and McPeek 2014). On one hand, the Unified Neutral Theory of Biodiversity explicitly assumes the dispersal ability of all individuals of all species to be symmetrical (Hubbell 2001). This implies no intrinsic variation among individuals for this trait, thus ruling out the possibility of dispersal being selectable. On the other hand, large number of studies have documented associations between morphological or life-history traits and dispersal distance of organisms in a population (Buoro and Carlson 2014; Stevens et al. 2013).This observation, coupled with the large body of theoretical literature on the subject (Cantrell et al. 2012; Hutson et al. 2003; Mathias et al. 2001; Travis and Dytham 2014), suggests that dispersal might be evolvable after all. While, in principle, this controversy should be resolved by experimental evolution studies, unfortunately that has not been the case.

In actively dispersing species, dispersal consists of two major processes: propensity (i.e. the tendency to leave the present habitat) (Friedenberg 2003) and ability (i.e. the ability to travel

through an inhospitable matrix) (Bitume et al. 2011). Experimental evolution studies have shown that the frequency of dispersers in a population can increase due to short-term selection (Friedenberg 2003; Ogden 1970). However, in the absence of knowledge about the dispersal ability, it is not clear whether the greater frequency of dispersers would actually translate into an increase in the dispersal distance of the organisms (although see Phillips et al. 2008). More critically, from a practical point of view, none of the experimental evolution studies have investigated whether the shape of the dispersal kernel (i.e. the distribution of the dispersal distance) (Nathan et al. 2012) evolves or not. Apart from its academic importance, knowledge of the dispersal kernel is crucial to predict range advance (Phillips et al. 2008), invasive potential (Kot et al. 1996), disease spread (Rappole et al. 2006) etc., and in general, most theoretical studies consider the kernel to be an evolutionarily static property of a species (Bianchi et al. 2009; Chapman et al. 2007; Krkošek et al. 2007 although see Starrfelt and Kokko 2010). This can lead to substantial under-estimation of the rate of spread of populations (Phillips et al. 2008), with potentially important economic consequences (Keller et al. 2009).

To investigate whether dispersal and dispersal kernel can evolve, we subjected four replicate laboratory populations of *Drosophila melanogaster* to directional selection for increased dispersal. After 33 generations of selection, we found that the frequency of dispersers in the population (i.e. propensity), as well as the mean distance travelled by the individuals (i.e. ability), and the rate of dispersal have increased significantly in the selected populations. Moreover, the shape of the dispersal kernel of the selected populations had significantly greater standard deviation, and reduced values of skew and kurtosis. Consequently, the selected populations had a greater proportion of long distance dispersers which translated into a 67%

increase in the spatial extent (Kot et al. 1996). Interestingly though, the evolution of higher dispersal did not lead to any cost in terms of the reproductive output of the selected individuals.

2. Materials and methods

2.1. Ancestral populations:

The experimental populations used in this study were derived from four independent large (breeding size of ~2400) laboratory populations of *Drosophila melanogaster* (DB_{1-4}) which in turn trace their ancestry to four outbred populations called JB_{1-4}. The detailed maintenance regime and ancestry of the JB_{1-4} populations has been described elsewhere (Sheeba et al. 1998). The maintenance regime of the DB_{1-4} populations are similar to the JB_{1-4}, except that the former set of flies are introduced into population cages on the 12^{th} day after egg collection.

From each DB_i population (where $i \in [1, 4]$), we derived two populations: VB_i (short for 'vagabond', subjected to selection for dispersal) and VBC_i (corresponding no-dispersal control). Thus VB and VBC populations that share a numerical subscript (e.g. say $VB_1$and VBC_1) were related by ancestry (DB_1 in this case), and hence were always assayed together and treated as blocks in statistical analyses.

2.2 Maintenance regime of experimental populations:

The adults of both VBs and VBCs were maintained in plexi-glass population cages (25 cm × 20 cm ×15 cm) at a high adult number (~2400 individuals) to avoid inbreeding. Following earlier protocols, both the larvae and the adults were maintained at 25°C and constant light conditions

(Sheeba et al. 1998). The flies were made to oviposit on petri-plates containing banana-jaggery medium for 12-16 hours. After oviposition, we cut small strips of the medium, each containing ~60-70 eggs, and introduced them individually into 35ml plastic vials that had ~6 ml of the same banana-jaggery medium. This ensured that the larvae were raised under low to moderate level of crowding, and there was no confounding effect of density-dependent selection (Joshi 1997). The adults started emerging by the 7^{th}-8^{th} day after egg collection and on the 12^{th} day, the VB populations underwent selection for dispersal (see below). Since at 25°C temperature, all normally developing adults eclose by 10^{th} -11^{th} day, our selection protocol ensured that there was no inadvertent selection for faster larval development (Prasad et al. 2001). After the imposition of selection, the flies were transferred to the population cages and immediately supplied with excess live yeast- paste to boost their fecundity. ~54hours after this, the flies were supplied with a fresh petri-plate containing banana-jaggery medium for oviposition. The eggs so collected formed the next generation and the adults were discarded, ensuring that adults from two different generations never co-exist. Thus, both VBs and VBCs were maintained under 15-day discrete generation cycles. For each VB population, we collected eggs in 80 vials (thus leading to approximately 4800 adults) while for VBCs, the corresponding number was 40. This ensured that after selection (see next section), the breeding population of the VB populations was equivalent to that of the VBCs,

2.3 Selection protocol

The apparatus for selection for dispersal consisted of three components: a *source*, a *path* and a *destination*. The source was an empty transparent cylindrical plastic container of diameter 11 cm

and height 16 cm with a funnel attached to one end (Fig. S1). The diameter of the broad end of the funnel matched that of the source, while the diameter of the exit to the stem was 1.8 cm. The path connecting the source with the destination consisted of a transparent plastic pipe of inner diameter ~1 cm. The destination was again a cylindrical plastic container (diameter 11 cm and height 16 cm) and contained a supply of moisture in the form of a strip of wet cotton. The end of the path protruded ~10 cm inside the destination (Fig. S1). This protrusion helped in reducing the rate of backflow as, after getting out of the path, the flies typically spend most of their time on the walls or floors of the container, and hence mostly failed to locate this aperture. To make the overall setup compact, the path was coiled (in the horizontal plane). The length of the path was 2 m at the beginning of the selection, but was increased periodically. By generation 33 (when most of the assays were done), the path length had reached 10 m.

In order to impose the selection, on the 12^{th} day after egg-collection, ~2400 adults (coming out of 40 vials) of a given VB_i population were placed in a source, which was then connected to the destination with the path. The entire setup was placed in a brightly lit room maintained at 25 °C. Since the source had no moisture, the flies were presumably under desiccation stress. Pilot runs with the ancestral DB populations had shown that under these environmental conditions, a subset of the flies tended to move through the opening towards the destination. Pilot studies also showed that very few flies dispersed in the presence of food in the source and therefore we decided to impose selection in the absence of food. The flies were allowed to disperse for six hours or till roughly 50% of the population reached the destination (whichever happened earlier). The arbitrary cut-off of six hours was chosen because assays in the lab had demonstrated that under desiccating conditions, there was almost no mortality during the first six hours (S. Tung

personal observations). Only the flies that reached the destination were allowed to breed for the next generation. Since the imposed selection allowed ~50% of the flies to breed, there were two independent "source-path-destination" setups, with ~2400 flies in the source, for each VB_i population. Post-selection, the dispersed flies in the two destination containers for a given VB_i population were mixed and transferred to a population cage. They were then supplied with live-yeast paste and after ~54 hours, eggs were collected (as mentioned above in section 2.2). The VBCs were maintained similarly as the VBs except two major differences. Firstly, after transferring the flies into the source, the exit was blocked by a cotton plug and the flies were allowed to desiccate for 3 hours (which was half the total time allowed for the VB flies to migrate). Following the protocol for the VB flies, the VBC flies were then supplied with a moist cotton plug for the next three hours. This controlled for the inadvertent desiccation experienced by the VB flies in the source and the path, as part of the selection protocol. It should be noted here that there was almost zero mortality in the VBC flies during this time, thus ensuring that the selection pressure for desiccation resistance was at best, mild. Secondly, all the flies in the VBC populations were allowed to breed, thus ensuring no selection for dispersal.

2.4 Assays:

All assays were performed after relaxing the selection on both VB and VBC populations for one generation. For this, the VB and VBC flies were transferred directly into the corresponding cages on the 12^{th} day after egg collection. The progeny of these flies, arising out of eggs collected on the 15^{th} day, were used for the assays. This common-rearing ensured that influence of phenotypic plasticity or non-genetic parental effects were ameliorated. Additionally, to remove any

extraneous influence due to larval crowding, egg density was kept to ~50 eggs on ~6mL food in each vial.

2.4.1 Dispersal kernel assay in presence and absence of food

This assay was used to assess the difference in dispersal propensity and ability between the VBs and the VBCs. The assay-setup was similar to the selection setup (see section 2.3, Fig S1) except for the length of the path, which was 20 m. Furthermore, to obtain the location kernel (i.e. the distribution of the location of the files after dispersal) the path was divided into multiple detachable sections: the first 20 sections were of length 0.5 m each and the next 10 sections were of length 1 m each. The destination container (a 250 ml plastic bottle) did not contain food or water but had a long protrusion to reduce backflow. On the 12^{th} day after egg collection, ~2000 adult flies were put into the source container and were allowed to disperse for 6 hours. During this interval, the entire setup was kept undisturbed under constant light and at a temperature of 25˚C. After the end of dispersal run, the setup was dismantled; the openings of the source, the destination, and each section of the path were secured carefully with cotton plugs, and labeled appropriately. The flies were then heat killed and the final location and sex of each fly was recorded. For each VB_i and VBC_i population, there were three such replicate kernel setups.

We performed two kinds of kernel assays: a) with an empty source and b) in the presence of ~20 ml banana-jaggery medium in the source. The former set of assays was performed after 19-20 generations of selection while the latter set of assays happened after 32-33 generations of selection. In total, this set of assays involved scoring ~96,000 flies.

2.4.2 Dispersal rate assay

Dispersal rate assay was performed after 39 generations of selection. To measure the rate of dispersal, the path distance was kept constant at 2 meters. A 100-mL glass flask (actual volume ~135 ml), with ~35 ml of banana-jaggery medium covering the bottom was used as the source, while the destination was a 250 ml plastic bottle. For every VB_i and VBC_i population, there were six replicate setups. Adults that were 12-day old (from egg-collection) were used for this assay. One day prior to the assay, we anaesthetized the flies under carbon-dioxide, separated them by sex and maintained them overnight at a density of 60 flies (30 males + 30 females) in vials containing ~6ml of banana-jaggery food. This ensured that the effects of adult crowding were controlled for and the flies had enough time to recover from stress due to anesthesia. Each assay was initiated by introducing 120flies (60 males+60 females) into each source. The total duration for this assay was 2 hours, with the destination being replaced with a fresh bottle after every 15 minutes. The flies in the destination at each time point were then heat-killed, segregated according to sex, and censused.

2.4.3 Fecundity assay

After 40 generations of selection, fecundity assay was performed on 14 day old flies (post egg collection), i.e. the day on which eggs were collected from the VB and the VBCs during their routine maintenance regime. The flies were segregated into pairs of 1 male + 1 female under mild CO_2 anesthesia and each pair was transferred into individual 50 ml falcon tubes. The falcon tubes had a small (~1.5 ml) food cup attached at the centre of the inner surface of the lid and had small pores on the tube wall to allow for exchange of gases.12 hours after introduction, the flies were discarded, and the number of eggs in each food cup was counted under microscope. 40 such

replicates were used for each of the eight selection× block combinations. The time window allowed for oviposition in this assay (12 hours) was the same as that used for the VBs and VBCs under their routine maintenance regime. Thus, we expected that a change in fecundity, if any, would be apparent in this time window.

2.4.4 Dispersal indices

2.4.4.1 Dispersal propensity

The proportion of flies that initiated dispersal was taken as dispersal propensity. Thus mathematically, propensity = (Number of flies found outside the source/ Total number of flies)

2.4.4.2 Dispersal ability

The dispersal ability was computed only on the flies that left the source, based on where (*i.e.* in which section of the path) they were found after 6 hours. All flies found in a given section of the path were deemed to have travelled the distance between the source and the midpoint of the section. The destination container was considered as a part of the last path-section. Thus mathematically,

$$Dispersal\ dis\tan ce = \sum_{i=1}^{30} \frac{x_i n_i}{Total\ number\ of\ \ flies\ outside\ source}$$

where, n_i is the number of flies found in the i^{th} path-section and x_i is the distance of the mid-point of this section from source.

Since dispersal ability is measured only on the flies that came out of the source, the measure of propensity and ability were independent of each other.

2.4.4.3 Dispersal rate

Dispersal rate was computed as the average time taken by the flies to cross the 2m path in the dispersal rate assay. Thus mathematically,

$$Time\ to\ disperse = \frac{\sum_i (i \times n_i)}{\sum_i n_i}$$

where, i ϵ [0.25, 2], with step size 0.25 and n_i is the number of flies that crossed a distance of 2m during the (*i- (i-0.25)*) hour interval.

2.4.5 Curve-fitting for estimating spatial extent

The data obtained from the dispersal kernel assay in presence of food, was fitted with the negative exponential distribution $y=ae^{-bx}$, where x is the distance from the source, *y* is the frequency of individuals found at *x*, and *a*, *b* are the intercept and slope parameters respectively. For this we pooled the data of the three replicates for each of the four populations of VB and VBC, estimated the frequency for each distance, natural log-transformed all values and fitted the equation ln(y) = ln(a) – bx using linear regression. The estimated R^2 values (Table S1) ranged between 0.67 and 0.99 and the residuals showed no major trends. The value of spatial extent was estimated as b^{-1}. ln (*a*/ 0.01), i.e. the distance from the source beyond which 1% of the population is expected to disperse.

During the linear regression, we observed that one data point in the kernel of the VB_3 population seemed to be an outlier. Excluding this point from the kernel considerably improved the fit (R^2 = 0.26 became R^2 = 0.91) and the distribution of the residuals improved considerably. However, removing this outlier reduced the mean value of the spatial extent of VBs from 32.6 m to 28.01m. Incidentally, there were no changes in terms of the statistical significance in the Mann-

Whitney U-tests for *a*, *b* or the spatial extent irrespective of whether the outlier is included or excluded. Therefore, in this study, we chose to report the value of spatial extent omitting the outlier. Note that this removal only makes our estimate of the spatial extent of VBs more conservative.

2. 5 Statistical analyses

Since VB_i and VBC_j that shared a subscript (*i.e.* $i = j$) were related to each other by ancestry, they were analyzed together as a block. Data for dispersal propensity, dispersal distance and dispersal rate were subjected to separate three factor mixed-model ANOVA with selection (VB and VBC) and sex (male and female) as fixed factors and block (1-4) as a random factor. The propensity data, being fractions, were arcsine-square root transformed (Zar 1999) before analysis. The standard deviation, skew, kurtosis, *a*, *b* and extent data for each population were computed after pooling the data for the three replicate kernels. For these six quantities we used separate Mann-Whitney U tests to compare the VBs and the VBCs. Since this is a non-parametric test, normality or homoscedasticity assumptions are not required. For the fecundity assay, we used two factor mixed-model ANOVA with selection (VB and VBC) as fixed factor and block (1, 2, 3 and 4) as a random factor. All statistical analyses were done using STATISTICA® v5 (StatSoft. Inc., Tulsa, Oklahoma).

3. Results and Discussion

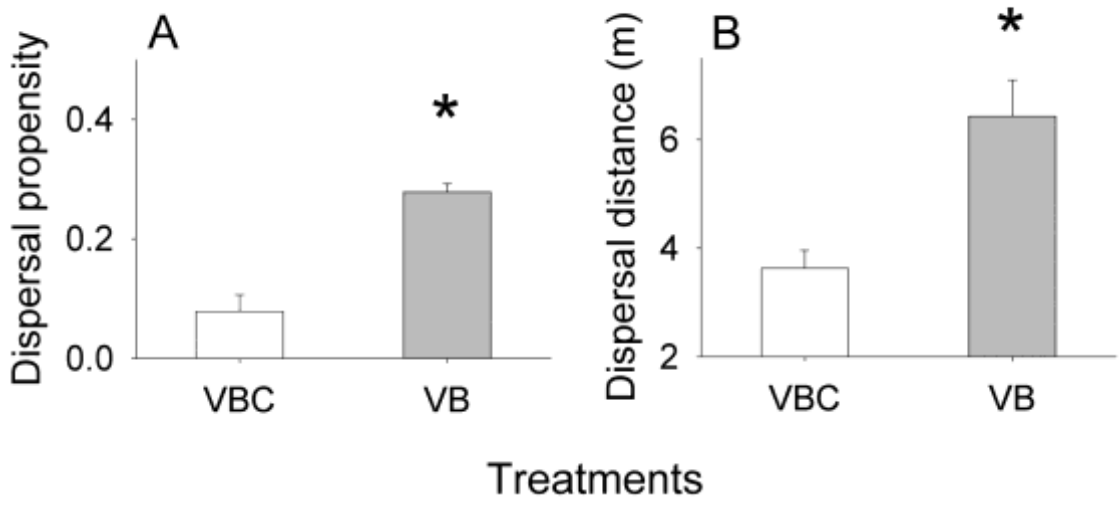

Fig. 1. **Mean dispersal propensity and dispersal distance.** (**A**) Propensity refers to the fraction of the total population that disperses from the source. (**B**) Ability refers to the mean distance travelled by those flies that come out of the source. The selected populations (VBs) had significantly greater propensity and ability compared to the controls (VBCs).The error bars represent standard errors around the mean and * denotes $P< 0.05$.

Dispersal propensity of the selected lines (VBs) was found to be significantly greater than the control populations (VBCs) (Fig. 1A, $F_{1, 3}=60.78$, $P=0.004$), which indicates that a larger fraction of the selected population were initiating dispersal. This is in line with previous studies that found that the proportion of dispersers in the population can go up due to selection for dispersal behavior (Friedenberg 2003; Ogden 1970).

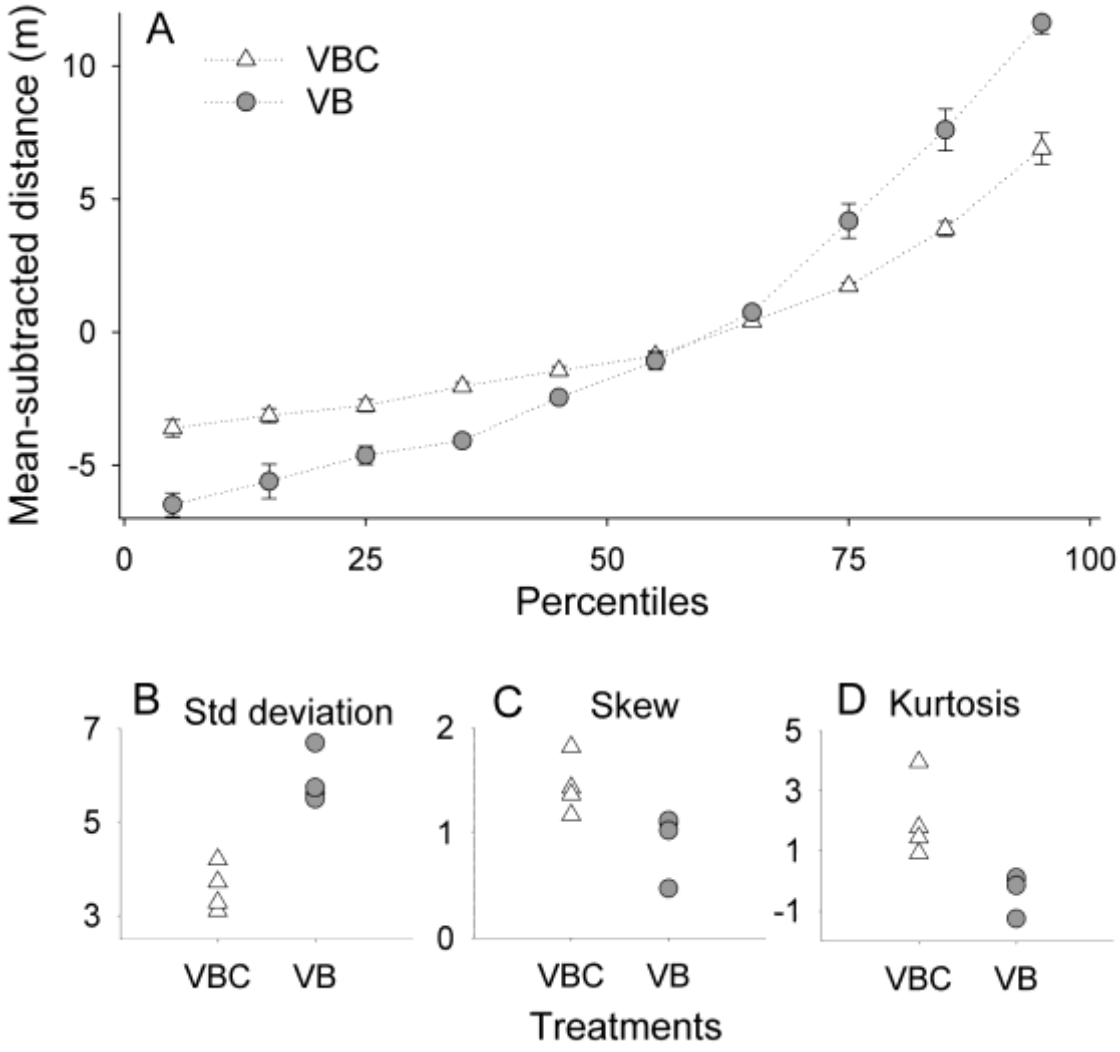

Fig. 2. Location and shape parameters of dispersal kernel for VB and VBC populations. (**A**) 5th to 95thpercentile for the mean-subtracted kernels of VB and VBC populations. The error bars represent standard errors around the mean. In few cases the error bars are too small to be visible. In terms of the upper (> 65) percentiles VB > VBC, while for the lower (<50 percentiles), VB < VBC. (**B**) Standard deviation, (**C**) Skew, (**D**) Kurtosis. Mann-Whitney U-tests suggested that the kernels of the VB populations had significantly larger standard deviation, less positive skew and lesser kurtosis (P= 0.02 for all) than the VBC populations. Together these indicate that the dispersal kernel of VBs have become flatter and their tails have become fatter.

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The average distance travelled by the dispersed flies (i.e. the ones that left the source) was considered to be a measure of their dispersal ability and the VBs were found to be superior to the VBCs in this aspect (Fig. 1B, $F_{1, 3}$=15.23, P=0.03). Since dispersal ability was measured only on the individuals that came out of the source, its magnitude was independent of the dispersal propensity of the populations. The evolution of both dispersal propensity and ability suggested that there was an actual difference in terms of the average distance traveled by the selected flies. This in turn implied that the kernel for the VB flies had evolved. The crucial question now was whether it was only the location parameters of the distribution that had been altered or had the kernel also evolved in terms of its shape.

Increase in mean distance travelled, in principle, can shift the kernel, without changing its shape. To eliminate this possibility, we subtracted the mean distance travelled in a given kernel replicate from the distance travelled by each individual in the replicate. We then computed the various percentiles of this data and found that all the higher percentiles (75 onwards) of VBs were higher than the corresponding percentiles of VBCs (Fig. 2A). This indicates the presence of greater number of Long-Distance-Dispersers (LDDs) (Nathan et al. 2012) in the selected populations and suggests that the overall kernel shape has changed. This conclusion was further strengthened by the observation that the VB populations had greater standard deviation (Fig. 2B), lesser positive skew (Fig. 2C) and more negative kurtosis (Fig. 2D) compared to the VBCs. This observation agrees with prior theoretical studies that predict the evolution of lower kurtosis and lower skew with increase in dispersal ability (Phillips et al. 2008).In order to compare the functional form of the dispersal kernel of VB and VBC populations, we fit the observed data with a negative exponential distribution, $y=ae^{-bx}$, where x is the distance from the source, y is the

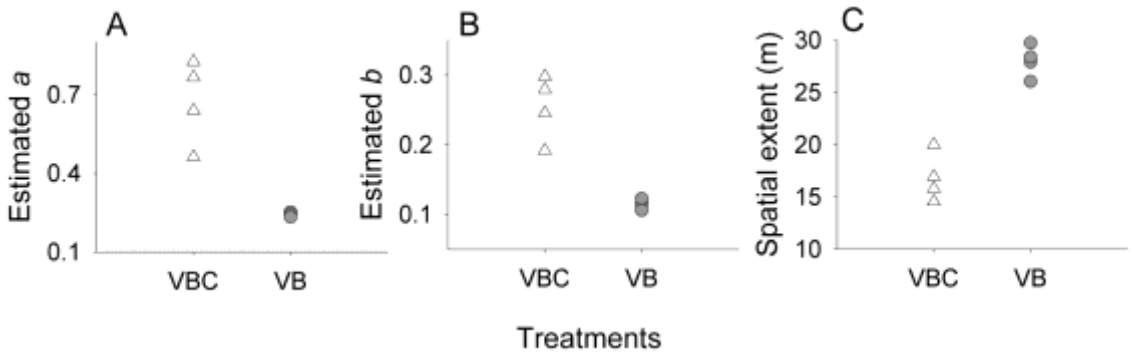

Fig. 3. Parameters of dispersal kernel and estimated spatial extent. Dispersal kernels of VBs and VBCs were fitted using the negative exponential $y=ae^{-bx}$, where x is the distance from the source and y is the frequency of individuals found at x. Estimated values of (**A**) a and (**B**) b are significantly lesser for VBs than VBCs (Mann-Whitney U tests, $P = 0.02$ for both). (**C**) Using the fitted curve, spatial extent of each of VB and VBC populations was computed by finding the distance from the source, beyond which 1% of the population is expected to reach. Spatial extents of VB > VBCs indicating fattening of the tail of the dispersal kernel and an increase in long distance dispersers in the population (Mann-Whitney U tests, $P = 0.02$).

frequency of individuals found at x, and a, b are the intercept and slope parameters respectively. We found that the values of a and b in case of the kernels of VB populations were significantly lower (Fig. 3A, 3B; see Table S1 for R^2 values) than the VBCs, indicating a general flattening of the shape and fattening of the tail of the kernel in the selected populations. This finding can have potential practical implications in terms of the distance over which a population can spread (Kot et al. 1996; Phillips et al. 2008). To get a better estimate of how this can affect the potential to disperse, we used the estimated average values of a and b to calculate the spatial extent (Kot et al. 1996) of the populations. Spatial extent refers to the distance from the source up to which an arbitrary fraction (here 1%) of the population are expected to reach (see section 2.4.5).The mean spatial extent of the VBs and VBCs were found to be 28m and 16.8m respectively (i.e. an

312 increase of 67%) which was due to an increase in the proportion of LDDs in the population (i.e.
313 the fatness of the tail of the distribution) (Fig. 3C).

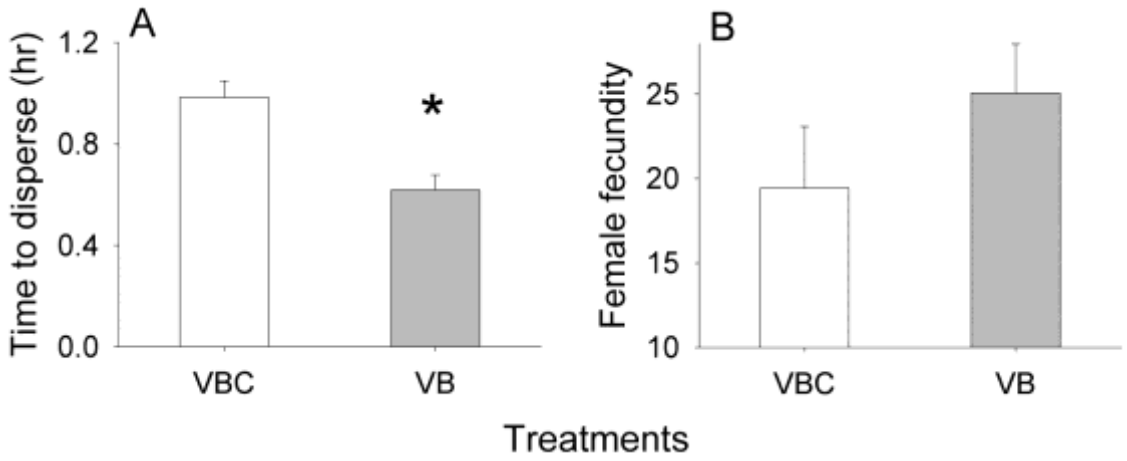

Fig. 4. Dispersal rate and female fecundity of VBs and VBCs. (**A**) Average (± SEM) time to disperse 2m for VB and VBC populations. VBs had significantly higher rate of dispersal. (**B**) Fecundity of VB and VBC populations were statistically not different from each other. * denotes $P<0.05$.

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315 Another major factor in the evolution of dispersal is the rate at which organisms travel during
316 dispersal (Phillips et al. 2010). This is particularly important for those organisms that disperse
317 actively through an inhospitable matrix, so as to reduce the amount of stress that they are
318 exposed to. This was true for the VB flies as there was no food or moisture in the path. We found
319 that the VB populations had significantly greater rate compared to the VBCs (Fig. 4A, $F_{1,}$
320 $_{3}=32.36$, $P=0.01$). Coupled with their greater dispersal ability, this observation suggested that the
321 selected flies had evolved not only behaviorally (i.e. propensity) but also physiologically (i.e.
322 ability and rate). Since both ability and dispersal rate are expected to be energy-intensive traits,
323 this naturally led to the question of physiological costs of evolution of dispersal.

Life-history theory suggests that enhancement in body-maintenance traits can often lead to trade off with reproductive output (Watson and Hoffmann 1996). Negative correlation between fecundity and dispersal ability have been empirically observed in several species of insects (Gu and Danthanarayana 1992b; Gu et al. 2006; Roff 1977).To check whether our selected flies experienced the same tradeoff, we assayed the fecundity of the flies on day 15, i.e. the same day on which they reproduced during selection. There was no significant difference between the fecundity of the VB and VBC flies (Fig. 4B, $F_{1,3}$=2.54, P=0.2), indicating an absence of a negative correlation between increased dispersal ability /and reproductive output.

Since some dispersal traits are known to vary across males and females in some *Drosophila* species (Markow and Castrezana 2000), we also analyzed the dispersal patterns for the two sexes separately. Although the male flies had significantly greater dispersal propensity ($F_{1,3}$=21.59, P=0.019), the dispersal ability ($F_{1,3}$=2.23, P=0.23) and rate ($F_{1,3}$=2.19, P=0.24) of both sexes were found to be comparable. More interestingly from an evolutionary point of view, the effect of selection was similar in both sexes in VBs and VBCs with no significant sex × selection effect for dispersal propensity (Fig. S2A, $F_{1,3}$=0.21, P=0.68), ability (Fig. S2B, $F_{1,3}$=2.19, P=0.24) or dispersal rate (Fig. S2C, $F_{1,3}$=0.46, P=0.55).We also investigated the dispersal kernels under conditions similar to the selection experiment (i.e. no food or water in the source). The results and inferences were similar to the case with food: the VB populations had significantly greater dispersal propensity (Fig. S3A, $F_{1,3}$=22.68, P=0.02), ability (Fig. S3B$F_{1,3}$=68.8, P=0.004) and rate ($F_{1,3}$=65.93, P=0.004, Fig. S3C) compared to the controls.

To the best of our knowledge, this is the first empirical study that demonstrates the simultaneous evolution of dispersal propensity, ability and speed and how that affects the evolution of the corresponding dispersal kernel. Given that the shape of dispersal kernel can evolve rapidly (33

generations in our case), it is important to consider dynamic kernels in predictions about advancement of invasion fronts (Kot et al. 1996), spread of disease vectors (Rappole et al. 2006) and range expansions (Phillips et al. 2008).Furthermore, although extant field studies have documented the high heritability of dispersal traits (Gu and Danthanarayana 1992a; Roff 1986), the connection between the evolution of these traits and the corresponding dispersal kernel is poorly understood. Moreover, relatively few studies consider the interaction of traits like propensity, ability and rate (although see (Phillips et al. 2010)) which is an important component in understanding the evolution of dispersal kernels in the field. Our study exerted a strong directional selection on dispersal propensity and ability. However, in nature, the direction and magnitude of the selection for dispersal might vary temporally and spatially, which can be a fruitful topic for both theoretical and empirical investigation.

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