Scaling up: understanding movement from individual differences to population-level dispersal

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Abstract

Dispersal is fundamental to life on our planet. Dispersal facilitates colonization of continents and islands. Dispersal mediates gene flow among populations, and influences the rate of spread of invasive species. Theory suggests that individuals consistently differ in dispersal propensity, however determining the relative contributions of environmental factors to individual and population-level dispersal, represent a major challenge to understand the spread of organisms. To address this, we conducted a field experiment using *Drosophila melanogaster*. As proxies for individuals with different dispersal propensities, we used wildtype strains of flies with natural variants of the *foraging* gene, known to influence dispersal in laboratory and field experiments. These included flies with *for*^{S} alleles known to be less dispersive, flies with the *for*^{R} alleles which are more dispersive flies as well as an outbred population established from field collected flies. We released approximately 6000 flies of each strain in an experimental arena (100 m x 100 m) in the field and our recaptures were used to determine dispersal of flies over time. To estimate environmental effects on dispersal, we measured temperature, wind direction and wind speed. Using partial-differential equations we combined ecological diffusion with advection to estimate dispersal rates and responses to wind. We found that temperature effects elicited a similar response in high and low dispersal lab strains with dispersal rate increasing with temperature most rapidly at temperatures above 18^{o}C. This was in contrast to outbred flies which remained unresponsive to temperature changes. We also detected a response to wind with advection rates increasing linearly with wind speed for all flies in general. Our results suggest that response to temperature and wind can minimize known differences in behavioural predispositions to disperse. Our results also suggest that the direction and magnitude of wind may play a key role in the colonization and distribution of fly populations. Our findings therefore have implications for forecasting the spread of pests and invasive species as well as pathogens and vectors of disease. Our findings further contribute to the understanding of how the environment can modify behavioural predispositions and to influence population-level dispersal in fly populations in particular and insect species in general.

Keywords: Movement ecology; dispersal; behaviour; individual variation; ecological diffusion; advection; *foraging* gene; *Drosophila melanogaster*.

1. Introduction

Dispersal plays a fundamental role in the evolutionary and ecological processes that govern life on our planet. From an evolutionary perspective, dispersal influences range expansion and rates of diversity (Bocxlaer et al. 2010) as well as adaptive radiations from mainland continents to islands. An example of the latter is the dispersal of anole lizards across the Greater Antilles that has facilitated the repeated evolution of similar ecomorphs on separate islands (Losos et al. 1998). Additionally, the evolution of Darwin's finches and Hawaiian honeycreepers involved a single dispersal event from the mainland that facilitated the subsequent evolution of many different forms across the archipelagos (Grant 1981; Freed et al. 1987). From an ecological perspective, dispersal influences rates of birth, death and immigration among populations and communities (Hanski and Gilpin 1991). Dispersal mediates gene flow among populations, and is an important consideration in studies of urbanized and fragmented landscapes (Cote et al. 2017, Edelsparre et al. 2018). Finally, dispersal can also influence the rate and severity of the spread of pathogens as well as invasive species (Kot et al. 1996).

Individuals within a population can disproportionally influence dispersal. Invasive cane toads from older established areas move slower and have reduced reproductive rates relative to individuals at the leading front of the invasion (Phillips 2009) which have longer legs, move faster and in straighter paths (Phillips et al. 2006). Increased dispersal rates of individuals which are at the leading front of invasions have also been observed in butterflies (Hill et al. 1999), aphids (Lombeart et al. 2014), and fish (Myles-Gonzalez et al. 2015). Understanding how individual variation contributes to population dispersal can have important implications for our ability to model and predict population level dispersal. A lack of understanding of the factors that affect dispersal can result in an underestimation of the spread of invasive species and the capacity for species to reclaim or colonize new habitats (Kot et al. 1996; Saastamoinen et al. 2018). This, in turn, limits our ability to make accurate ecological forecasts (Clarke

et al. 2001), which affects our ability to manage the effect of spread of invasive species on ecosystems that are being invaded or colonized (Hastings et al. 2005; Gomez-Uchida et al. 2018).

Elucidating the underlying factors that contribute to dispersal is a major challenge for the field of movement ecology (Nathan et al. 2008; Cote et al. 2017). Several morphological, physiological, and behavioural traits are linked with variation in dispersal. For example, insect wing dimorphisms that affect dispersal ability are common (e.g. pea aphid: Zera and Deno 1997; rice plant hoppers: Brisson 2010). Behavioural traits have also been linked with dispersal in a wide range of animal taxa, including birds, fishes, and lizards (Réale et al. 2007; Cote et al. 2017). Individuals have been shown to differ in their dispersal propensity depending on whether they are aggressive (Duckworth and Badyaev 2007), are risk takers (Edelsparre et al. 2013), or are sociable (Cote and Clobert 2007). In rare cases, genes that underlie the link between these behaviours and dispersal have been identified (Korsten et al. 2013; Edelsparre et al. 2014) offering unique insights into the potential mechanisms contributing to individual differences in dispersal. However, how such factors play out in nature to influence dispersal at the population-level is poorly understood (Gurarie et al. 2009).

There are three main hypotheses through which population-level variation in dispersal might arise. First, individuals within populations can differ in their predispositions to disperse if genetic differences between individuals affect dispersal directly or via differences in morphology, physiology and/or behaviour, such as those mentioned above (Sastaamoinen et al. 2018). Under this hypothesis we would expect populations to display consistent individual differences in dispersal across multiple environmental contexts (changes in climate and/or landscape). Such consistent differences could exist even if groups or individuals with different dispersal predispositions responded similarly (parallel responses) and/or differently (divergent responses) to environmental change. Second, variation in dispersal could arise largely in response to environmental factors. This could be if dispersal

predispositions are absent or if the environmental effects are strong enough to minimize dispersal predispositions. Under this scenario we would expect to see a general population response to the environment and with changes in the environment driving changes in dispersal (each disperser is a random draw from the population). Finally, variation in dispersal could arise through a combination of the above possibilities, including conditions ranging between individual (e.g. dispersal predispositions) and environmentally driven dispersal. Detecting complex relationships between key factors such as those outlined above would require the implementation of dynamic models that are capable of estimating the relative contribution of each factor on the movement process (Hefley et al. 2017; Hooten and Hefley 2019).

In the following study we set out to address these three hypotheses by combining individual-level predictors and environmental data in dynamic models designed to assess the relationship between each factor over time. In our experiment, we used the common fruit fly, *Drosophila melanogaster*, a convenient organism to model dispersal in general and to investigate individual-level predictors of dispersal in particular. To accomplish this we first produced a large outbred study population from field collected flies. Secondly, we incorporated individual-level predictors of dispersal by using *Drosophila melanogaster* that carry variants of a gene known to influence differences in the propensity of the adult fly to disperse (Edelsparre et al. 2014; Edelsparre et al. 2018). This particular *Drosophila* system consists of two strains of flies that differ in several movement related behaviours both as larvae and adults and these differences are mediated by natural variation in the *foraging* (*for*) gene (Osborne et al. 1987; de Belle et al. 1993; Pereira and Sokolowski 1993; Edelsparre et al. 2014). Individuals that carry for^R alleles (rovers) are active foragers as larvae and more dispersive as adults while individuals that carry for^s alleles (sitters) tend to be less active foragers as larvae and less dispersive as adults. Recent laboratory experiments demonstrated environmentally dependent plasticity in dispersal propensity of the rover and sitter variants of the *foraging* gene (Anreiter and Sokolowski 2019, Edelsparre et al.

2020). Consequently, the rover and sitter strains were used to examine how different dispersal propensities may interact with the environment to produce population-level dispersal and the outbred population was used to examine how a population with multiple dispersers respond to the environment.

Temperature and wind are two important environmental factors that influence insect activity and movement in nature (Glick 1942; Taylor 1963; McManus 1988). Work on several insect species suggests that there are critical temperatures below which insects will not initiate dispersal (Taylor 1963) and even lower temperatures beyond which insects are not able to sustain flight (Cockbain 1961). In general, insect dispersal will increase with temperature, likely with some optimal temperature range conducive to movement. However, whether such a response can be linked with dispersal predispositions remain largely unexplored. Although, wind direction and speed are thought to be critical to insect flight the behavioural response to wind is likely not a simple one (McManus 1988). Since the early 1920's, when large numbers of insects were first recorded in the atmospheric convective layer (Glick 1939), researchers held the view that aerial dispersal was entirely dependent on weather conditions (e.g. passive dispersal; McManus 1988). Most empirical data since then suggested that there is a behavioural component to dispersal. For example, using radars to quantify airflow and movement of small insects in the atmosphere, Wainwright et al. (2017) detected movement velocities independent of airflow. Work on flies is consistent with the findings of Wainwright et al. (2017). Desert species of *Drosophila* (*D. mimica*, *D. nigrospiracula* and *D. mojavensis*) disperse both up and down wind and this behaviour is dependent on food availability (Richardson and Johnston 1975; Markow and Castrezana 2000). In a recapture experiment, Coyne et al. (1982) released groups of *D. melanogaster* and its sister species *D. simulans* in the Death Valley and were able to recapture a proportion of them at an oasis several miles from the release site even though the flies faced cross winds during their flight. Although none of the studies on *Drosophila* explicitly tested wind effects on dispersal the results suggest that, for these flies, dispersal is not entirely passive. As is the case for the

effects of temperature on dispersal, it is unknown whether individual flies respond similarly to wind effects or whether there is a behavioural predisposition to respond differently to wind speed and direction.

Here we examined the effects of temperature, and wind direction and speed on the dispersal behaviour of rover and sitter *D. melanogaster* as well as on an outbred population of flies released in the field using a mark/release/recapture experiment. Because flies do not exhibit dispersal behaviour in a strict sense (e.g. departure, settlement), but rather move while foraging, searching for mates, avoiding predators etc. we defined any movement away from a release site as dispersal. This idea fits well with dispersal defined in its simplest form as any movement by individuals leading to spatial spread with potential for genetic mixing (Ronce 2007). We quantify dispersal as the rate at which this spread occurs (see analysis below). To investigate how the dispersal behaviour of rover, sitter and the outbred strain of flies respond to temperature and wind we monitored the weather during the experiment. We explicitly evaluated the general prediction that dispersal increases with temperature and whether our more (rover) and less (sitter) dispersive strains differed from our outbred population. We also explicitly tested whether flies use wind to disperse and we used a novel approach to detect the tendency for flies to disperse either up or down wind in the field. We also determined whether the strains differed in their dispersal in response to wind, both in terms of direction and velocity. Combining individual predictors of dispersal with temperature and wind allowed us to evaluate not only the interaction between individual dispersal propensity and the environmental factors, but also the relative contribution of each factor in population-level dispersal in nature.

2. **M**aterials and methods

2.1 Fly lines

To evaluate how strain-differences in behaviour influence dispersal of flies in the field we used two inbred strains (rover- *for*^{R} and sitter- *for*^{s}) and one outbred strain of flies. The effect of *for* on the dispersal strategy of the rover and sitter inbred strains was documented in Edelsparre et al. (2014) and Edelsparre et al. (2018). The outbred population was established from 92 iso-female lines originally collected in Sudbury, Ontario, Canada (501484.97 E, 5143198.65 N UTM) on August 12, 2012 by Thomas Merritt. Several months prior to the commencement of the field experiment each of the 92 lines were randomly assigned to one of 6 170mL sponge-topped plastic *Drosophila* bottles (4 bottles each containing 15 different lines and 2 bottles each containing 16 lines) containing 40 mL of media as described below and maintained as stocks. Two months prior to the field experiment the six bottles were transferred to population cages and flies were allowed to mix for one generation in 16 open bottles inside the population cage. Hereafter the 16 bottles were extracted from the cage, and brooded over for two more generations before a fresh generation of flies was used in the field experiment.

2.2 Experimental field

To quantify the movement of flies in the field, we prepared a 100 m by 100 m large experimental arena in an open meadow at the ***rare* Charitable Research Reserve** west of Cambridge, Ontario, Canada (553195.00 E, 4802841.00 N UTM) that was recently converted from agricultural land to a nature reserve (Fig. 1a). The field is flat with a sloping gradient of zero from corner to corner and mainly consists of vegetation such as goldenrods (*Solidago* spp.), asters (*Symphyotrichum* spp.), thistles (*Circium* spp), and common milkweed (*Asclepias syriaca*). Vegetation reached an average height of approximately 40-50 cm and the density was largely uniform across the entire field (personal observation).

198 The experimental design was constructed with sampling points positioned in a gradient radiating away
199 from a central site from which the flies were released. The arrangement of each point was determined
200 by first specifying a 21 × 21 matrix with 441 points (corresponding to 100 × 100 metre square with
201 each point 5 m apart) and then by selecting specific points at which sampling locations were to be
202 placed. Locations were selected by first converting Cartesian coordinates to polar coordinates using a
203 trigonometric function that varied sampling concentration according to a cosine function and truncating
204 the continuous values such that positive values represented sampling locations and negative values
205 represented locations without sampling. This resulted in a total of 227 locations (including the central
206 release location) that varied in distance and density in a parameterized gradient (Fig. 1b). Arranging
207 sampling locations in this manner was done to balance the spatial resolution with the amount of time
208 required to sample the entire field (i.e. temporal resolution).
209
210 The experimental arena was prepared by first positioning each of the four corners 100 m apart in the
211 field and then building trap lines within the arena. The arena was 100 × 100 m^2 with 21 rows and 21
212 columns. Trap lines were positioned every 5 m. Stake flags (6.35 × 8.89 cm on a 53 cm wire stem,
213 Milwaukee Tools) were placed at 5 m intervals along each trap line resulting in 441 flagged locations.
214 The field diagram (Fig. 1b) was used to identify flags where a given sampling location was to be
215 placed. One of the four corners of the arena was angled towards a North-Easterly direction. This was
216 due to the prevailing winds mainly moving in an East and East-North-East direction as measured by
217 our weather station (Vantage Vue, Davis Instruments, California, USA). For the same reason, the
218 release site at coordinate (0,0) was off-set from the middle to allow higher sampling resolution in the
219 direction of the prevailing winds. The weather station was installed along the diagonal (Fig. 1c) to
220 measure wind direction and speed and temperature every 15 minutes.
221

Sampling locations consisted of baited traps inserted into the ground (10 cm off ground). Traps were prepared from a 90 mL plastic cup (Starplex, Starplex Scientific, Toronto, ON, Canada) positioned horizontally on a small piece of bamboo (Figure 1d). Prior to inserting a trap, the sampling location was prepared by manually removing vegetation around the flag and placing a small piece of landscaping fabric (The Scotts Company LLC) on the ground surface. To prevent other insects such as ants from gaining access to a trap, the small piece of bamboo that held the trap was inserted through the inner part of a two-part plastic shot glass (81.3 mL Amscan, Toronto, ON, Canada). The outer part of the glass was filled with water, which served as a moat and effectively prevented access to the piece of bamboo holding the baited trap (Fig. 1d).

Each trap was baited with 20 mL of fly medium consisting of a mixture of sugar, dead yeast and agar. Briefly, for approximately 1 L of medium we mixed 100 g of sugar, of which 50% of the sugar came from sucrose and the other 50 % came from bananas (~0.12 g of sucrose in 1 g of banana) that were blended prior to mixing, with 110g of yeast and 17.43 g of agar in 1 L of tap water. We also added 8 g of $C_4H_4KNaO_6$, 1 g of KH_2PO_4 and 0.5 g each of NaCl, $MgCl_2$, $CaCl_2$ and $Fe_2(SO_4)_3$ which was part of the standard yeast-sugar-agar laboratory medium that we used for maintaining fly stocks (Belay et al. 2007). All compounds were combined, mixed for an hour and autoclaved to ensure that the medium was sterile before being applied to traps. In a preliminary study in the laboratory, banana-baited traps were not biased towards any strain or sex used in the present study (results not shown).

2.3 Counting and marking flies

Each fly strain was counted and marked with a unique fluorescent pigment (see Edelsparre et al. 2014 for a full description of the marking technique). To estimate the number of flies we created a standard curve for the relationship between the number of flies and weight for each strain separately. This was done by counting and weighing batches of 50, 100, 150, 200, and 450 flies and estimating the linear

regression equation for each strain. Each equation was used to predict the number of flies in each vial given their group weight and strain ID. Batches of approximately 150 flies were anesthetized with CO_2 and transferred to separate empty plastic vials after which a minute amount of dry fluorescent pigment (DayGlo, Cleveland, OH, USA) was added (rover, Saturn Yellow, AX-17-N; sitter, Aurora Pink, AX-5-11; outbred flies, Horizon Blue, A-19). The colours were assigned randomly to each strain and were not known to the experimenters. Each vial was gently shaken to ensure that all flies were rolled in the pigment and subsequently transferred to 170 mL sponge-topped plastic *Drosophila* bottles where they were allowed 24 hours to groom themselves. This method left a badge on the ventral and dorsal thoraces that can be visualized by a portable black light in the field. In total 5644 rovers, 5352 sitters and 5657 outbred flies (2-7 days post eclosion) were tagged and released at the centre of the experimental field.

2.4 Releasing and recapturing flies

Prior to release, flies were acclimatized to their surroundings by placing the *Drosophila* bottles next to the central release trap at 09:00 on 10 October 2015. At 12:00 flies were released by gently removing the sponge-tops from each bottle in a haphazardly chosen order. It took 8 minutes from the release of the first bottle to the release of the last bottle.

Recapturing flies involved first randomly choosing between rows and columns of the trapping arena (Fig. 1b). Once either rows or columns were selected, three field observers sampled rows or columns in a random order. A complete sampling round involved visiting all 227 baited traps and bringing traps containing captured flies to a central location where all the samples were processed. Processing involved transferring flies to transparent *Drosophila* vials, identifying the colour markings by exposing flies to a black light and visually counting the number of flies with each colour at each sample location. After processing, the flies were transferred back to their respective baited trap and released at their

capture location. Traps were baited with fresh food every second day. The first sampling round commenced 30 minutes after release (12:30), and we strove to complete a minimum of two sampling rounds per day over a course of five days (or until no or few flies remained on the experimental field). A sampling round took a maximum of two hours depending on how many flies were captured. In total 12 sampling rounds were completed over the 5 days, however, because of low capture rates after 50 hours post-release we used the first six sampling rounds in our analysis corresponding to 0.5, 1.5 , 21, 26, 46 and 50 hours after the release (Fig. 2).

2.5 Data analysis

To investigate how the rover, sitter and outbred strains respond to temperature and wind in the field, we developed and fit a dynamic spatio-temporal model to the data shown in Fig. 2. Dynamic spatio-temporal modelling enables mathematical models, like partial differential equations, to be fit to data using commonly applied parameter estimation techniques (Wikle et al. 2019; Hooten and Hefley 2019).

For each fly-strain, we fit a partial differential equation that included a component that describes ecological diffusion and a component that describes advection. By fitting a model to each strain separately we are able to evaluate how individual-level predictors (i.e. rover/sitter differences) translate to population-level processes. The partial differential equation can be written as

$$\frac{\partial}{\partial t}u(\mathbf{s},t) = \left(\frac{\partial}{s_1^2} + \frac{\partial}{s_2^2}\right)\mu(\mathbf{s},t)\,u(\mathbf{s},t) + \left(\frac{\partial}{s_1} + \frac{\partial}{s_2}\right)\nu(\mathbf{s},t)\,u(\mathbf{s},t)\ . \quad \text{Eq. 1}$$

In Eq. 1, $u(\mathbf{s},t)$ is the likelihood an individual is at location $\mathbf{s} \equiv (s_1\ , s_2\ )'$ at time t, which can be converted to the intensity of the dispersing population by multiplying $\theta \times u(\mathbf{s},t)$, where θ is the number of individuals released (i.e., 5644 rovers, 5352 sitters and 5657 outbred flies). The diffusion rate, $\mu(\mathbf{s},t)$, and advection rate, $\nu(\mathbf{s},t)$, can vary over both space and time and depend on environmental covariates (e.g., temperature and wind).

For the analysis, we specified the diffusion rate as follows

$$\mu(\mathbf{s},t) = \begin{cases} e^{\alpha_0 + \alpha_1 z(\mathbf{s},t)} & x(t) = 1 \\ 0 & x(t) = 0 \end{cases}, \quad \text{Eq. 2}$$

where α_0 is the intercept and α_1 is a regression coefficient for standardized temperature, $z(\mathbf{s},t)$, at location $\mathbf{s}$ and time t. The indicator variable $x(t)$ depends on the time, t, and is equal to 1 if it is daylight and equal to zero if it is night. When it is night we assume that the flies do not move (Konopka and Benzer 1971), thus the diffusion rate should be equal to zero. When it is daylight, the diffusion rate should always be greater than zero, thus motivating the exponential function used in Eq. 2. The standardized temperature was calculated by subtracting the mean temperature from the observed temperature and dividing this by standard deviation. Thus, the intercept term, α_0, represents the natural log of the diffusion rate at the average temperature recorded during the study. Finally, temperature was measured at a single location, thus $z(\mathbf{s},t)$ is spatially constant (i.e., $z(\mathbf{s},t) \equiv z(t)$.

Similarly, we specified the advection rate as

$$v(\mathbf{s},t) = \begin{cases} \beta_1 w(\mathbf{s},t) & x(t) = 1 \\ 0 & x(t) = 0 \end{cases}, \quad \text{Eq. 3}$$

where β_1 is a regression coefficient for wind velocity, $w(\mathbf{s},t)$, at location $\mathbf{s}$ and time t. During daylight, the advection rate, $v(\mathbf{s},t)$, can be positive or negative. Thus, there is no constraint required like the exponential function in Eq. 2. If the wind transports (advects) individuals, we expect a positive advection rate, whereas if individuals actively move into the wind then we expect a negative advection rate. Unlike the diffusion rate, the advection rate does not contain an intercept term because when the wind velocity is zero (i.e., $w(\mathbf{s},t) = 0$)), there should be no advection. Similar to temperature, wind velocity was measured at a single location, thus $w(\mathbf{s},t)$ is spatially constant.

By fitting Eq. 1 to the data for each strain, we are able to estimate parameters that describe each strain's movement in response to changes in the environment. For example, the magnitude and sign of the estimated value of α_1 allows us to infer how the diffusion rate for each strain changes when the temperature increases. We provide a brief description below of how we fit partial differential equations to data. A more detailed description is provided in supporting material along with computer code (see Appendix S1).

Fitting Eq. 1 to the data from each strain first involves specifying a statistical model for the observed data. We assumed

$$y_i(\mathbf{s}_j, t) \sim \text{negative binomial}\left(\lambda_i(\mathbf{s}_j, t), \phi\right) \quad , \quad \text{Eq. 4}$$

where $y(\mathbf{s}_j, t)$ is the number of individual of strain i ($i = 1,2,3$) captured at the location $\mathbf{s}_j$ corresponding to the trap locations (i.e., $j = 1,2, \ldots ,227$) at the time t. For our data, the observed times were $t = 0.5, 1.5, 21, 26, 45,$ and 50 hours post release (see Fig. 2). For a given trap location and sampling time, the expected number of individuals caught from each strain was $\lambda_i(\mathbf{s}_j, t)$ which was modeled with

$$\lambda_i(\mathbf{s}_j, t) = \begin{cases} \mathrm{p}_i \theta_i u_i(\mathbf{s}_j, t), & with\ proability\ \psi_i \\ \mathrm{p}_i \theta_i \dfrac{1}{|\mathcal{S}|}, & with\ probability\ 1 - \psi_i \end{cases} \quad . \quad \text{Eq. 5}$$

In Eq. 5, p_i is the capture probability, $\theta_i u_i(\mathbf{s}_j, t)$ is the intensity of the dispersing population from the Eq. 1 (where θ_i is the known number of individuals of strain i released), $\frac{1}{|\mathcal{S}|}$ is a uniform probability density where $|\mathcal{S}|$ is the area of my study regions, and ψ_i is a mixture probability. Conceptually, Eq. 5 represents a population where, upon release, a proportion, ψ_i, of the individuals' movement is described by Eq. 1 and the movement of the remaining proportion of individuals $(1 - \psi_i)$ is described by a uniform distribution over the study area. The proportion of individuals with movement that follow

the uniform distribution exhibit abnormal behaviour and could be caught with equal chances at any location within the study area. For example, upon release a small proportion of the flies exhibited bolting behaviour. Because these behaviours are abnormal, we expected that the estimated value of the parameter ψ_i would be close to one.

We took a Bayesian approach for parameter estimation and specified priors for all unknown parameters. To estimate the parameters in our model from the data, we developed software using a Markov chain Monte Carlo algorithm similar to the approach described in Hooten and Hefley (2019, Ch 28 pg. 501); however, solving Eq. 1 involved developing an emulator described by Hooten et al. (2011). Details of the implementation are provided in Appendix S1.

3. **R**esults

In total, we captured 1223 rovers, 861 sitters and 279 outbred flies over the five days of the experiment. Approximately 95% (2363 flies) of all captured flies were captured within the first 50 hours of the experiment, corresponding to the first six sampling rounds. The capture data from the six sampling rounds used in the analysis are described in Figure 2. During the first 50 hours from release, the flies experienced a range of changing weather conditions, ranging from 10-22 ^{o}C during the day and nightly temperatures ranging from just above 5 ^{o}C to 16 ^{o}C (Fig. 3a). Wind speeds ranged from 0 to just above 2.5 m/s (Fig. 3b) with wind direction predominantly between 120 and 140 degrees, corresponding to East-North-East and East-South-East directions (Fig. 3c).

In general, our prediction that dispersal increased with temperature was supported. This conclusion is based on the finding that the posterior mean of the diffusion rates for rovers and sitters increased rapidly from 18 ^{o}C to 22 ^{o}C (Fig. 4). The posterior distribution of the diffusion rates show that dispersal

of both sitters and rovers responded positively to temperature, but the magnitude of the response is uncertain, particularly at temperatures above 20 ^{o}C. In addition, the posterior mean estimates for rovers and sitters mirrored each other particularly at temperatures below 18 ^{o}C, but tended to be greater than the diffusion rate for outbred flies, which largely remained unchanged across the temperature range (Fig. 4). For example, if the temperature was 22 ^{o}C over a course of 24 hours, our results indicate that we should expect rovers and sitters to spread 79 m^2 and 152 m^2 more when compared to the outbred strain. Conversely, at temperatures below 14 ^{o}C the outbred strain spreads at least 36 m^2 more over 24 hours when compared to rovers and sitters. The posterior distribution for all parameter estimates for the temperature analysis are shown in Fig. 6a and 6b.

Wind speed and direction played a significant role in dispersal for all three fly strains. This conclusion is supported by the finding that the advection parameter was positive and increased with wind speed for rovers, sitters and outbred flies (Fig. 5). In fact, even with the level of uncertainty around each posterior mean the lower limit of the 95 % credible interval for all three strains remains above zero even at wind speeds below 0.5 m/s. Although there is uncertainty in the estimates (cf. 95 % credible intervals on Fig. 5), the difference among posterior mean responses becomes larger as wind speed increases. For example, sitters were most sensitive to wind speeds whereas rovers were the least sensitive; at a wind velocity of 1 m/s sitters are expected to advect approximately 5 metres further over 24 hours than rovers, however, at wind velocities of 2.5 m/s the difference between the two strains is expected to be approximately 13 metres over 24 hours. The parameter estimates for the advection part of the analysis are shown in Fig. 6c.

4. **D**iscussion

A number of conclusions can be drawn from the results of our study. First, temperature plays a critical role in fly dispersal in the field. We found that for rovers and sitters, the posterior mean of the diffusion rates increased with temperature particularly between 18 and 22 ^{o}C. In contrast, the posterior mean of the diffusion rate of the outbred fly strain tended to be greater than the diffusion rates of rovers and sitters at temperatures less than 18 ^{o}C, but largely remained unchanged across the temperature range. The rover and sitter responses to temperature mirror each other. However, the effect size of the mean estimates particularly between the rover and the outbred strain is noteworthy. For example, at 22 ^{o}C the mean diffusion rate is nearly four times larger for rovers than for the outbred strain (Fig. 4), suggesting that the models have the capacity to predict strain-dependent differences in dispersal outcomes over time. Second, wind plays a critical role in the dispersal of flies. The advection rate increased linearly with wind speed for all strains, however, rovers tended to be less sensitive to the effect of wind speed relative to sitters and outbred flies. As was the case for temperature, there is a relatively large amount of uncertainty in the magnitude of the response of sitters, rovers and outbred flies to wind speed, as indicated by the 95 % credible intervals, however, there is strong evidence that all three strains responded positively to increasing wind speed. In addition, the posterior mean advection distance between rovers and sitters more than doubled for every 1 m/s increase in wind speed (Fig. 5). This suggests that flies were influenced by both the direction and the speed of wind during the experiment, but that the magnitude of this effect tended to depend on fly-strain. This suggests that differences in down wind dispersal were due to behavioural differences and not a passive response. Thirdly, combining ecological diffusion modelling with wind advection clearly improved our ability to predict dispersal at the population-level. This conclusion is based on the finding that dispersal of flies in the field varied with both temperature and wind. For temperature, the posterior means of the diffusion rates increased rapidly for rovers and sitters, while the rate remained unchanged for the outbred population. For wind the effect is even stronger. The posterior means of the advection rates were above zero across the range of wind speeds for all three strains. Even with the level of uncertainty in the estimates, the

lower limit of the 95 % credible intervals for all three posterior means is above zero at low wind speeds. This further strengthens the evidence in favour of a strong wind effect. Although there was some evidence of differences in response to wind speed, overall rovers, sitters and the outbred population exhibited similar patterns of response to wind (parallel responses). Taken together the environmental effects were strong for both the rover and sitter strains as well as the outbred population, although the strength of the evidence varied across the temperature and wind ranges. Our models therefore captured the effects of key descriptors of fly movement that a model without temperature and wind likely would have ignored and therefore our results inform our understanding of potential factors underlying dispersal in nature.

Climate driven environmental conditions such as temperature and wind have long been considered key factors influencing fly dispersal in particular and insect dispersal in general (Glick 1941, McManus 1988). Since the 1950's prognoses of the relationship between temperature, wind, and dispersal have been used to both forecast and backtrack incidents of migrant pests such as African armyworms and desert locusts (Wellington 1954, Rainey 1979). In support of this, we found that wind speed and direction played a significant role in dispersal even at extremely low wind speeds. This suggests that wind transport can underlie a large part of the estimated rate of dispersal. We detected wind speeds between 0 and 3 m/s during this study. As such, wind may play an even larger role when speeds exceed 3 m/s. Clearly, in our study flies were able to navigate towards, around and into the traps. Taylor (1974) used the term "boundary layer" to describe a hypothetical layer of air near the ground where wind is not able to affect the movement of small insects (i.e. insect flight speed exceeds wind speed). Such a layer would allow flies to navigate towards and around traps. In our study, the wind above this boundary layer may have facilitated the dispersal of flies prior to visiting a particular trap, but whether or not the wind effect was mediated by behaviour (as a means to conserve energy) or remained passive

cannot be directly answered by our data. Nevertheless, the low wind speeds and moderate to warm temperatures experienced during our study were conducive to insect movement (Glick 1942, Cockbain 1961, Taylor 1963).

Our findings demonstrate the potential use of genetic and environmental information in detecting individuals that may influence dispersal disproportionally. Although we did not address genetic effects directly in this study, we used different strains of flies, rovers (more dispersive) and sitters (less dispersive) and an outbred strain, to understand how flies with different genetic predispositions to disperse influenced the spatial spread of a fly-population. Unlike previous findings in the laboratory and the field (Edelsparre et al. 2014, Edelsparre et al. 2018), the known difference in dispersal between rovers and sitters was minimized in response to temperature and wind conditions. Sitters tended to disperse faster with wind than did rovers particularly at high wind speeds. This suggests that an understanding of dispersal likely hinges on disentangling how genes involved in dispersal interact with relevant factors in the environment to affect individual differences in dispersal behaviour (Sokolowski 2001, Dudaniec et al. 2018, Saastamoinen et al. 2018). Insect movement involves multiple genes (Saastamoinen et al. 2018) in interaction with many environmental factors including temperature and wind measured in the present study. *for* is one of the genes that affects movement related behaviours in a wide range of insect species, including ants (Ingram et al. 2005) and honey bees (Ben-Shahar et al. 2002). *for* has also recently been associated with outbreaks of locusts (Tobbak et al. 2013) and possibly spruce budworm, *Choristoneura fumiferana* (Van Hezewijk et al. 2018). Describing the role of *for* and other candidate genes in invasive species should provide a unique opportunity to better understand and model invasion biology in terrestrial environments. Additionally, by extending this thinking to include temperature and wind our findings are particularly pertinent to elucidating conditions under which climatic factors may influence insect invasions. Specific predictions regarding climatic effects on insect

463 dispersal offer the potential to reduce uncertainty in invasion biology where unpredictability seems to
464 be the rule rather than the exception (Melbourne and Hastings 2009).
465
466 Our findings provide a powerful framework for combining individual-level predictors with climate
467 driven variables to understand dispersal at the population-level. An implicit assumption in many
468 models, including diffusion models, is that the dispersing individuals within the population are
469 identical (Kot et al. 1996, Gurarrie et al. 2009). Other studies have proposed individual differences in
470 behaviour as an explanation for non-random variation in dispersal frequently reported in the literature
471 (Skalski and Gilliam 2000, Fraser et al. 2001, Réale et al. 2007). We addressed this assumption directly
472 by using the rover, sitter and outbred strains of flies as proxies for individual differences in dispersal
473 propensity. Through the fitting of separate models for each strain we show how such efforts can be
474 useful predictors of population-level dispersal in the field. Our results are consistent with models that
475 propose individual variation in behaviour as explanations for population-level variation in dispersal.
476 Our findings not only provide the potential to inform how individuals influence dispersal
477 disproportionally but they also improve our understanding of key mechanisms surrounding individual
478 differences in response to environmental factors that give rise to population-level dispersal.
479
480 There are potential limitations to our study. First, the temporal resolution we used in our experimental
481 design affected the power of our analysis. Increasing temporal sampling over spatial sampling could
482 have provided stronger evidence for differences among strains. One way to increase the temporal
483 resolution may be to sample flies as presence/absence data rather than abundance. This would reduce
484 the time spent at each sampling location and increase the number of times the entire arena could be
485 surveyed in a day. Second, the rover and sitter strains have been cultured in the laboratory for over 30
486 years and may not have recapitulated dispersal behaviour in natural populations. The dispersal rate of
487 rovers and sitters above 18 ^{o}C showed a response to temperature consistent with insect flight activity

488 reported in the literature (Cockbain 1961, Taylor 1963). Along with the rover and sitter strains, we
489 released an outbred strain established from the field. This strain was assembled in 2015 using 92
490 isofemale lines collected in 2012. The diffusion rate of this outbred strain was stable across the
491 temperature range in comparison to the rover and sitter strains. The outbred strain was collected near
492 the limit of *D. melanogaster's* northern-most distribution in Sudbury Ontario, Canada (Thomas Merritt,
493 personal communication). This might explain why the outbred strain tended to be more active at low
494 temperatures than the rover and sitter strains that were originally caught well within *D. melanogaster's*
495 normal range (Toronto, Ontario, Canada, 402 km south of Sudbury). Overall, our results provide a
496 useful approach for investigating how behavioural differences might lead to dispersal outcomes for a
497 population with multiple dispersal strategies and how those strategies may interact with temperature
498 and wind.
499
500 Our study provides two scientific contributions to our understanding of the evolution and ecology of
501 organismal movement. First, we took advantage of the wealth of information available for flies in
502 general and this *Drosophila melanogaster* model system in particular to build models that incorporated
503 genetic variation known to underlie dispersal strategy (Edelsparre et al. 2014, Edelsparre et al. 2018)
504 and climatic effects. Earlier attempts to understand the movement of organisms generally relied on
505 simpler analyses of linear rates of spread involving individuals with equal dispersal propensity
506 (Hastings 2005, Cote et al. 2017). A long history of publications rooted in the ecology of organismal
507 movement illuminate a far more complex and interesting process and over the last two decades
508 researchers have pushed for an integration of behavioural and environmental data with movement
509 theories expressed as mathematical models (Hastings et al. 2005, Nathan 2008, Hefley et al. 2017). In
510 line with this idea, our results clearly demonstrate that more complex models indeed can be critical to
511 capturing factors that influence animal movement at the individual level (i.e. multiple dispersal
512 strategies) and highlight the importance of matching theoretical models of movement with data to

513 better understand the distribution of organisms in nature. Second, we developed a powerful framework
514 for linking individual variation in dispersal strategy with the environment. Understanding how such
515 components can lead to population-level dispersal is valuable because individual differences in
516 behaviour are increasingly linked with important ecological and evolutionary processes such as habitat
517 fragmentation (Cote et al. 2017), climate change (Fitzpatrick and Edelsparre 2018), and biogeography
518 (Canestrelli et al. 2016). In fact, individual variation in behaviour has recently been referred to as a
519 'pacemaker' of evolution of non-behavioural traits. Our study therefore offers a unique opportunity to
520 understand how dispersal strategy influences the distribution of populations and ultimately the pattern
521 of biological diversity on our planet (Canestrelli et al. 2016).
522
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524
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References

Anreiter, I. and M. B. Sokolowski. 2019. The *foraging* gene and its behavioral effects: pleiotropy and plasticity. Annual Review Genetics. 53: 373-392.

Belay, A. T., R. Scheiner, A. K. -C. So, S. J. Douglas, M. Chakaborty-Chatterjee, J. D. Levine and M. B. Sokolowski. 2007. The *foraging* gene of *Drosophila melanogaster*: spatial-expression analysis and sucrose responsiveness. *Journal of Comparative Neurology*. **504**: 570-582.

Ben-Shahar Y., A. Robichon, M. B. Sokolowski, and G. E. Robinson. 2002. Influence of gene action across different time scales on behavior. *Science*. **296**: 741–744.

Brisson, J. A. 2010. Aphid wing dimorphisms: linking environmental and genetic control of trait variation. *Philosophical Transactions of the Royal Society B*. **365**: 605-616.

Bocxlaer, I. V., S. P. Loader, K. Roelants, M. Menegon and F. Bossuyt. 2010. Gradual adaptation toward a range-expansion phenotype initiated the global radiation of toads. *Science*. **327**: 679-682.

Canetrelli, D., R. Bisconti and C. Carere. 2016. Bolder takes all? The behavioral dimension of biogeography. *Trends in Ecology and Evolution*. **31**: 35-43.

560 Clarke, J. S., S R. Carpenter, M. Barber, S. Collons, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual,
561 R. Pielke Jr., W. Pizer, C. Pringle, W. V. Ried, K. A. Rose, O. Sala, W. H. Schlesinger, D. H. Wall and
562 D. Wear. 2001. Ecological forecasts: an emerging imperative. *Science*. **293**: 657-660.
563
564 Cote, J. and J. Clobert. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of*
565 *the Royal Society B*. **274**: 383-390.
566
567 Cote, J., E. Bestion, S. Jacob, J. Travis, D. Legrand and M. Baguette. 2017. Evolution of dispersal
568 syndromes in fragmented landscapes. *Ecography*. **40**: 56-73.
569
570 Cockbain, A. J. 1961. Low temperature thresholds for flight in *Aphis fabae* Scop. *Entomologia*
571 *Experimentalis et Applicata*. **4**: 211-219.
572
573 Coyne, J. A., I. A. Boussy, T. Prout, S. H. Bryant, J. S. Jones and J. A. Moore. 1982. Long-distance
574 migration of *Drosophila*. *The American Naturalist*. **119**: 589-595.
575
576 Denno, R. F., Roderick, G. K., Olmstead, K. L., & Döbel, H. G. 1991. Density-related migration in
577 planthoppers (*Homoptera: Delphacidae*): the role of habitat persistence. *The American Naturalist*. **138**:
578 1513-1541.
579
580 Duckworth, R. A. and A. V. Badyaev. 2007. Coupling of dispersal and aggression facilitates the rapid
581 range expansion of a passerine bird. *Proceedings of the National Academy of Sciences USA*. **104**:
582 15017-15022.
583

584 Dudaniec, R. Y., C. J. Yong, L. T. Lancaster, E. I. Svensson, and B. Hansson. 2018. Signatures of local
585 adaptation along environmental gradients in a range-expanding damselfly (*Ischnura elegans*).
586 *Molecular Ecology*. **27**: 2576–93.
587
588 Edelsparre, A. H., M. J. Fitzpatrick, M. A. Rodríguez and M. B. Sokolowski. 2020. Tracking dispersal
589 across a patchy landscape reveals a dynamic interaction between genotype and habitat structure. *Oikos*.
590 DOI: https://doi.org/10.1111/oik.07368.
591
592 Edelsparre, A.H., McLaughlin, R.L. & Rodríguez, M.A. 2013. Risk taking not foraging behavior
593 predicts dispersal of recently emerged stream brook charr (*Salvelinus fontinalis*). *Ecosphere*. **4**: 73.
594
595 Edelsparre, A. H., S. Shahid and M. J. Fitzpatrick. 2018. Habitat connectivity is determined by the
596 scale of habitat loss and dispersal strategy. *Ecology and Evolution*. **8**: 5508-5514.
597
598 Edelsparre, A. H., A. Vesterberg, J. H. Lim and M. J. Fitzpatrick. 2014. Alleles underlying larval
599 foraging behaviour influence adult dispersal in nature. *Ecology Letters*. **17**: 333-339.
600
601 Fitzpatrick, M. J. and A. H. Edelsparre. 2018. The genomics of climate change. *Science*. **359**: 29-30.
602 Freedman, L. A., S. Conant and R. C. Fleischer. 1987. Evolutionary ecology and radiation of Hawaiian
603 passerine birds. *Trends in Ecology and Evolution*. **2**: 196-203.
604
605 Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le and G. T. Skalski. 2001. Explaining leptokurtic
606 movement distributions: intrapopulation variation in boldness and exploration. *The American*
607 *Naturalist*. **158**: 124-135.
608

609 Garlick, M. J., J. A. Powell, M. B. Hooten and L. R. McFarlane. 2012. Homogenization of large-scale
610 movement models in ecology. *Bulletin of Mathematical Biology*. **73**: 2088-2108.
611
612 Glick, P. A. 1939. The distribution of insects, spiders, and mites in the air. *United States Department of*
613 *Agriculture Technical Bulletin*. **673**: 1-151.
614
615 Glick, P. A. 1942. *Insect population and migration in the air*. pp. 88-98 in Moulton, S. (Ed.),
616 Aerobiology. American Association of Advanced Science. Washington, D.C. A.A.A.S. Publ. 17.
617
618 Gomez-Uchida, D., D. Canas-Rojas, C. M. Riva-Rossi, J. E. Ciancio, M. A. Pascual, B. Ernst, E. Aedo,
619 S. S. Musleh, F. Valenzuela-Aguayo et al. 2018. Genetic signals of artificial and natural dispersal
620 linked to colonization of South America by non-native Chinook salmon (*Oncorhynchus tshawytscha*).
621 *Ecology and Evolution*. **00**: 1-18.
622
623 Grant, P. R. 1981. Speciation and the adaptive radiation of Darwin's finches. *American Scientist*. **69**:
624 653-663.
625
626 Gurarie, E., J. J. Anderson and R. W. Zabel. 2009. Continuous models of population-level
627 heterogeneity inform analysis of animal dispersal and migration. *Ecology*. **90**: 2233-2242.
628
629 Hanski, I. and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain.
630 *Biological Journal of the Linnean Society*. **42**: 3-16.
631

632 Hastings, A., K. Cuddington, K. F. Davies, C. J. Dugaw, S. Elmendorf, A. Freestone, S. Harrison, M.
633 Holland, J. Lambrinos et al. 2005. The spatial spread of invasions: new developments in theory and
634 evidence. *Ecology Letters*. **8**: 91-101.
635
636 Hefley, T. J., M. B. Hooten, R. E. Russel, D. P. Walsh and J. A. Powell. 2017. When mechanism
637 matters: Bayesian forecasting using models of ecological diffusion. *Ecology Letters*. **20**: 640-650.
638
639 Hilbe, J. M. (2011). *Negative Binomial Regression*. Cambridge University Press.
640
641 Hill, J. K., C. D. Thomas, D. S. Blakeley. 1999. Evolution of flight morphology in a butterfly that has
642 recently expanded its geographic range. *Oekologia*. **121**: 165-170.
643
644 Hooten, M. B., M. J. Garlick, and J. A. Powell. 2013. Computationally efficient statistical differential
645 equation modeling using homogenization. *Journal of Agricultural, Biological, and Environmental*
646 *Statistics*. **18**: 405-428.
647
648 Hooten, M. B., Leeds, W. B., Fiechter, J., & Wikle, C. K. (2011). Assessing first-order emulator
649 inference for physical parameters in nonlinear mechanistic models. *Journal of Agricultural, Biological,*
650 *and Environmental Statistics*. **16**: 475-494.
651
652 Hooten, M.B. and T.J. Hefley. 2019. *Bringing Bayesian Models to Life*. Chapman and Hall/CRC.
653 Ingram K. K., P. Oefner, D. M. Gordon. 2005. Task-specific expression of the foraging gene in har-
654 vester ants. *Molecular Ecology*. **14**: 813–818.
655

656 Johnson, C. G. 1969. *Migration and Dispersal of Insects by Flight*. Methuen & Co Ltd. London. 763
657 pp.
658
659 Konopka, R. J. and S. Benzer. 1971. Clock mutants of *Drosophila melanogaster*. *Proceedings of the*
660 *National Academy of Sciences of the United States of America*. **68**: 2112-2116.
661
662 Korsten, P., T. van Overveld, F. Adriaensen and E. Matthysen. 2013. Genetic integration of local
663 dispersal and exploratory behaviour in a wild bird. *Nature Communications*. **4**: 2362.
664
665 Kot, M., M. A. Lewis and P. van den Driessche. 1996. Dispersal data and the spread of invading
666 organisms. *Ecology*. **77**: 2027-2042.
667
668 Lombaert, E., A. Estoup, B. Facon, B. Joubart, J. C. Grégoire, A. Jannin, A. Blin, and T. Guillemaud.
669 2014. Rapid increase in dispersal during range expansion in the invasive ladybird *Harmonia axyridis*.
670 *Journal of Evolutionary Biology*. **27**: 508-517.
671
672 Losos, J. B., T. R. Jackman, A. Larson, K. de Queiros and L. Rodríguez-Schettino. 1998. Contingency
673 and determinism in replicated adaptive radiations of island lizards. *Science*. **279**: 2115-2118.
674
675 Markow, T. A. and S. Castrezena. 2000. Dispersal in cactophilic *Drosophila*. *Oikos*. **89**: 378-386.
676 Melbourne, B. A., and A. Hastings. 2009. Highly variable spread rates in replicated biological
677 invasions: fundamental limits to predictability. *Science*. **325**: 1536-1539.
678

McManus, M. L. 1988. Weather, behaviour and insect dispersal. *Memoirs of the Entomological Society of Canada*. **146**: 71-94.

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

Myles-Gonzalez, E., G. Burness, S. Yavno, A. Rooke and M. G. Fox. 2015. To boldly go where no goby has gone before: boldness, dispersal tendency, and metabolism at the invasion front. *Behavioural Ecology*. **26**: 1083-1090.

Nathan, R. 2008. An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences of the United States of America*. **105**: 19050-19051.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz and P. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*. **105**: 19052-19059.

O'Riain, M. J., J. U. M. Jarvis and C. Faulkes. 1996. A dispersive morph in the naked mole rat. *Nature*. **380**: 619-621.

Osborne, K. A., A Robichon, E. Burgess, S. Butland, R. A. Shaw, A. Coulthard, H. S. Pereira, R. J. Greenspan and M. B. Sokolowski. 1987. Natural behavior polymorphism due to a cGMP-dependent protein kinase of *Drosophila*. *Science*. **227**: 834-836.

703 Phillips, B. L. 2009. The evolution of growth rates on an expanding range edge. *Biology Letters*. **5**:
704 802-804.

705

706 Phillips, B. L., G. P. Brown, J. K. Webb and R. Shine. 2006. Invasion and the evolution of speed in
707 toads. *Nature*. **439**: 803.

708

709 Rainey, R. C. 1979. *Interactions between weather systems and population of locusts and noctuids in*
710 *Africa*. pp. 109-119. In Rabb, R. L. and G. G. Kenedy (Eds.), Movement of highly mobile insects:
711 concepts and methodology in research. North Carolina State Univ. Raleigh. 455 pp.

712

713 Réale, D., S. M. Reader, D. Sol, P. T. McDougall and N. J. Dingemanse. 2007. Integrating animal
714 temperament with ecology and evolution. *Biological Reviews*. **82**: 291-318.

715

716 Richardson, R. H. and J. S. Johnston. 1975. Behavioral components of dispersal in *Drosophila mimica*.
717 *Oecologia*. **20**: 287-299.

718

719 Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution.
720 *Annual Review of Ecology, Evolution and Systematics*. **38**: 231-253.

721

722 Saastamoinen, M., G. Bocedi, J. Cote, D. Legrand, F. Guillaume, C. W. Wheat, E. A. Fronhofer, C.
723 Garcia, R. Henry, A. Husby, et al. 2018. Geneticsof dispersal. *Biological Reviews*. **93**: 574–599.

724

725 Skalski, G. T. and J. F. Gilliam. 2000. Modeling diffusive spread in a heterogeneous population: a
726 movement study with stream fish. *Ecology*. **81**: 1685-1700.
727
728 Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika*. **38**: 196-218.
729
730 Sokolowski, M. B. 2001. Genetics meets behaviour. *Nature Reviews Genetics*. **2**: 879-890.
731
732 Sokolowski, M. B., C. Kent and J. Wong. 1984. *Drosophila* larval foraging behaviour: developmental
733 stages. *Animal Behaviour*. **32**: 645-651.
734
735 Taylor, L. R. 1963. Analysis of the effect of temperature on insects in flight. *Journal of Animal*
736 *Ecology*. **32**: 99-117.
737
738 Taylor, L. R. 1974. Insect migration, flight periodicity, and the boundary layer. *Journal of Animal*
739 *Ecology*. **43**: 225-238.
740
741 Tobback, J., H. Verlinden, K. Vuerinckx, R. Vleugels, J. Vanden Broeck & R. Huybrechts. 2013.
742 Developmental-and food-dependent *foraging* transcript levels in the desert locust. *Insect Science*. **20**:
743 679–688.
744
745 Van Hezewijk B., D. Vertman, D. Stewart, C. Béliveau, and C. Cusson. Environmental and genetic
746 influences on the dispersal propensity of spruce budworm (*Choristoneura fumiferana*). 2018.
747 *Agricultural and Forest Entomology*. **20**: 433-441.
748

749 Wainwright, C. E., P M. Stepanian, D. R. Reynolds and A. M. Reynolds. 2017. The movement of small
750 insects in the convective boundary layer: linking pattern with process. *Scientific Reports*. **7**: 5438.
751
752 Wellington, W. G. 1954. Atmospheric circulation processes and insect ecology. *The Canadian*
753 *Entomologist*. **86**: 312-333.
754
755 Wikle, C. K. 2003. Hierarchical Bayesian models for predicting the spread of ecological processes.
756 *Ecology*. **84**: 1382-1394.
757
758 Wikle, C.K., A. Zammit-Mangion, and N. Cressie. 2019. *Spatio-Temporal Statistics with R*. Chapman
759 and Hall/CRC.
760
761 Zera, A. J. and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects.
762 *Annual Review of Entomology*. **42**: 207-230.
763
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771 Figures

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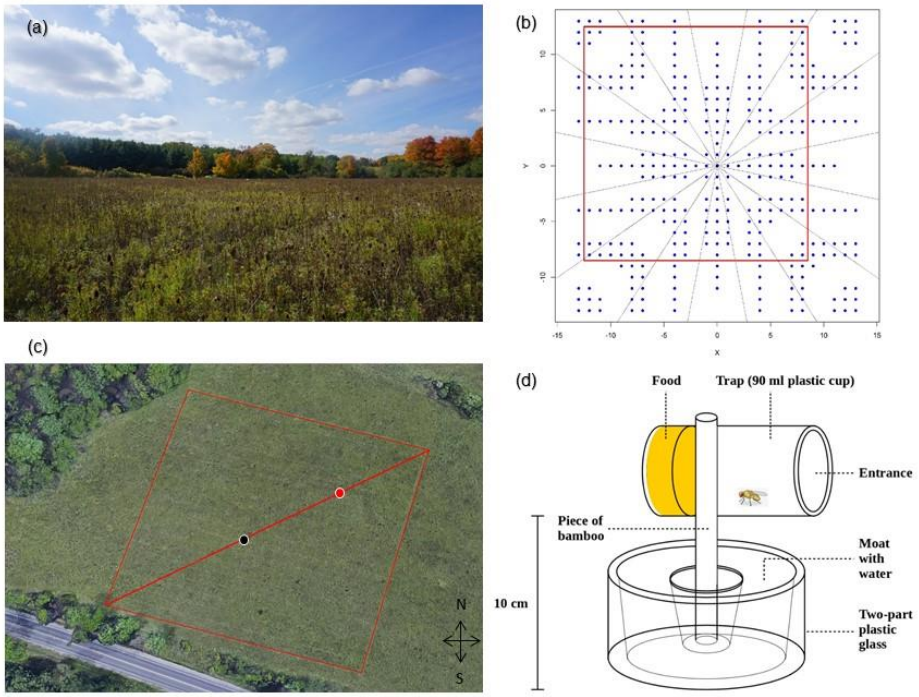

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774 Figure 1.

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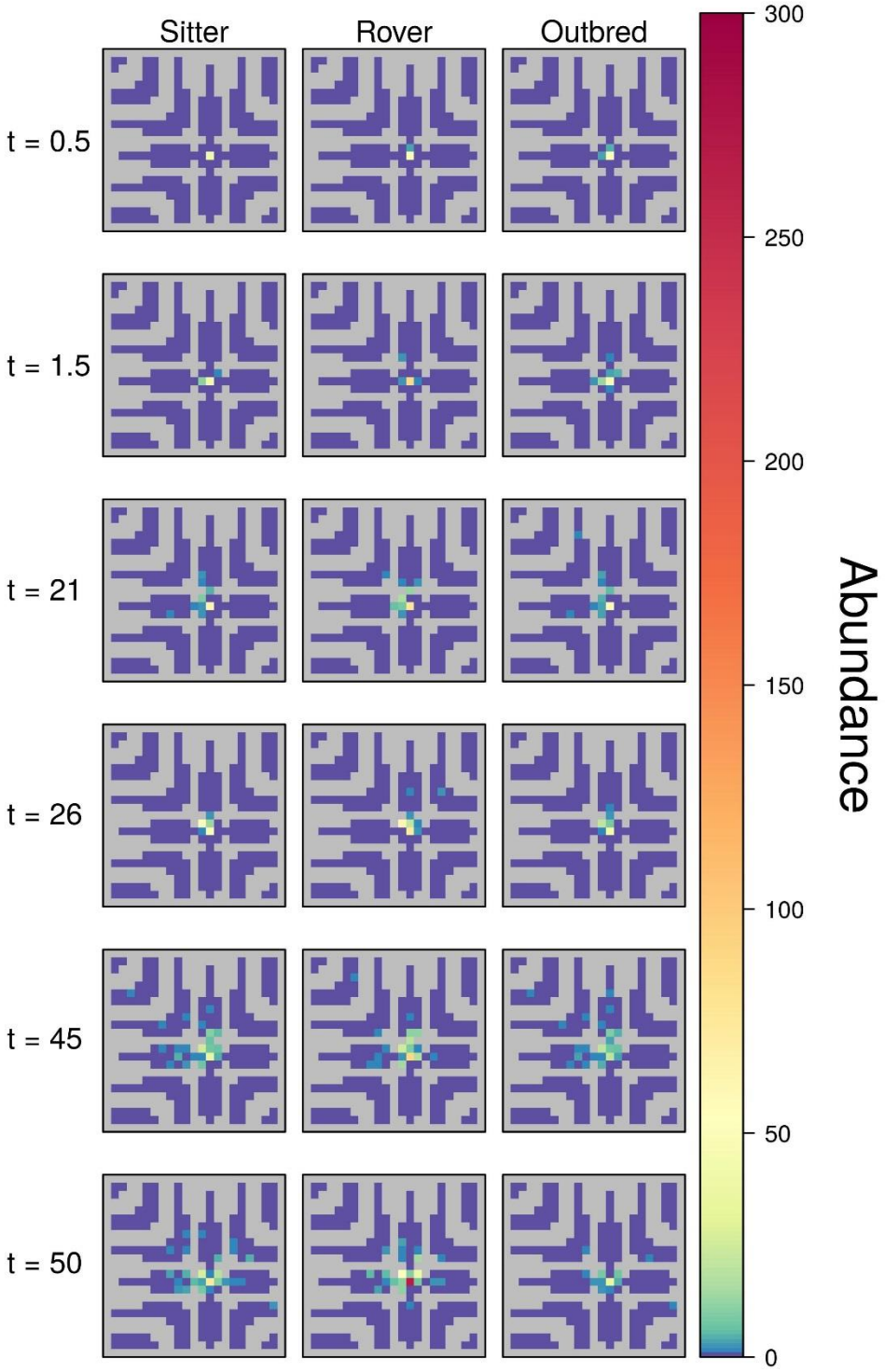

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784 Figure 2.

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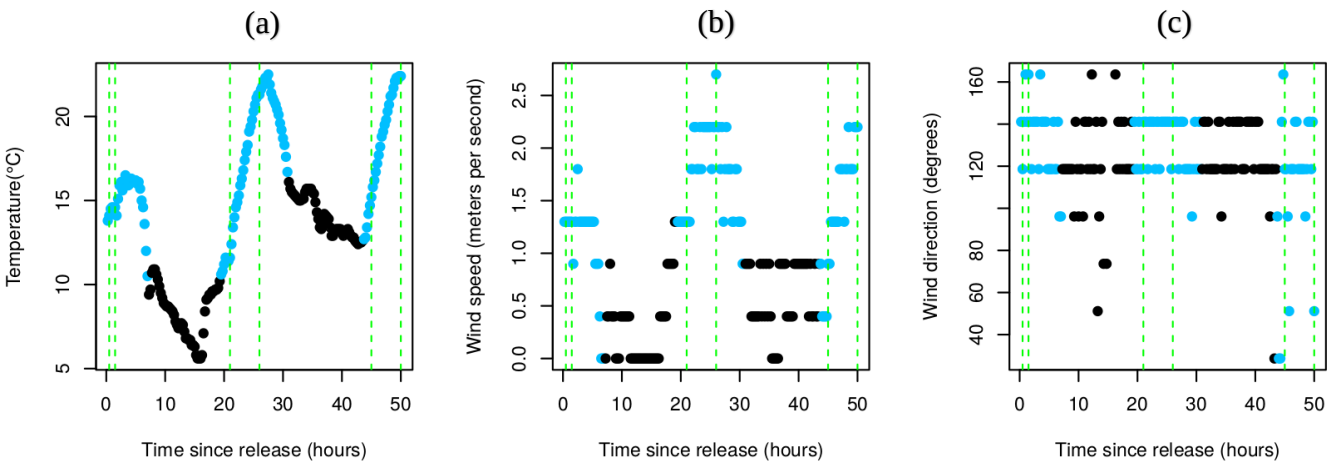

Figure 3.

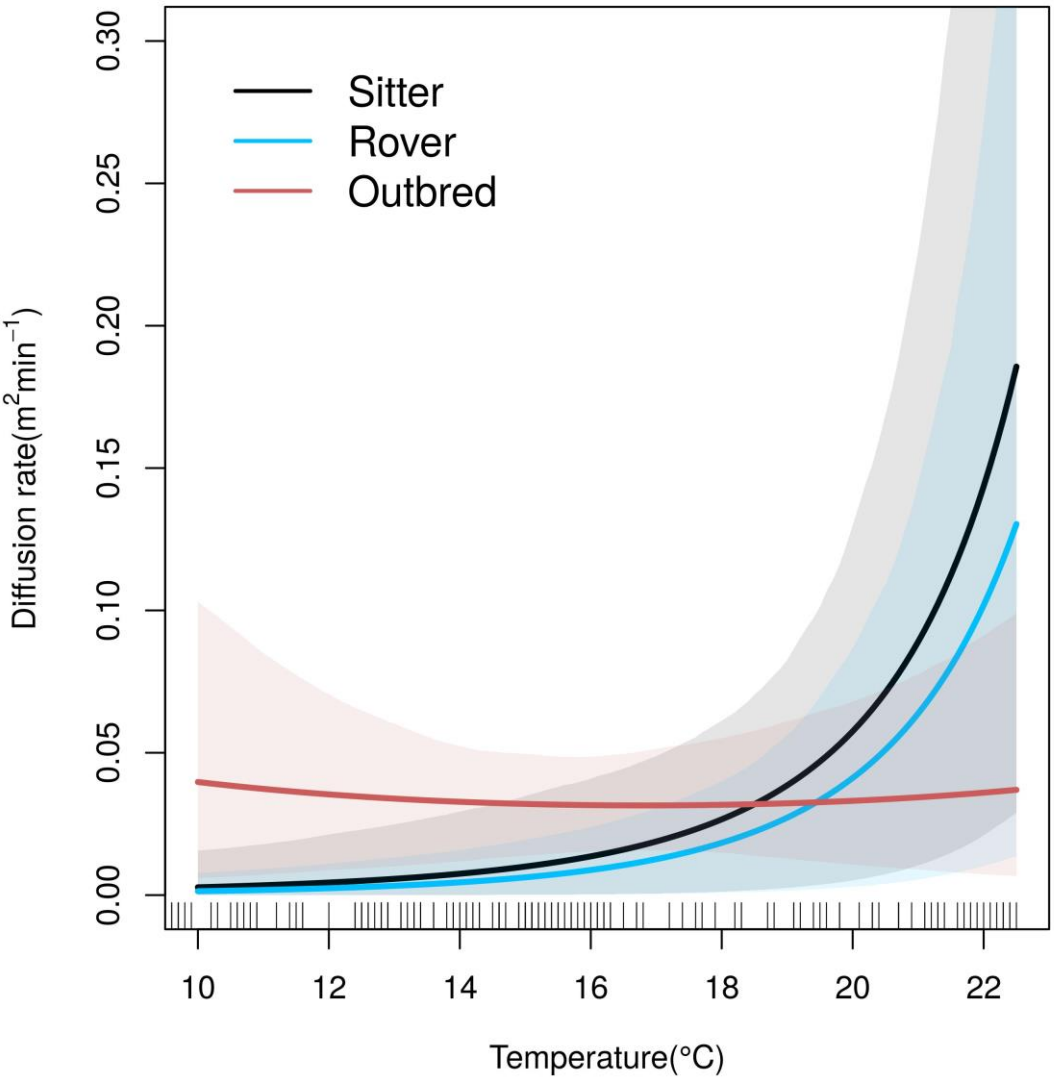

Figure 4

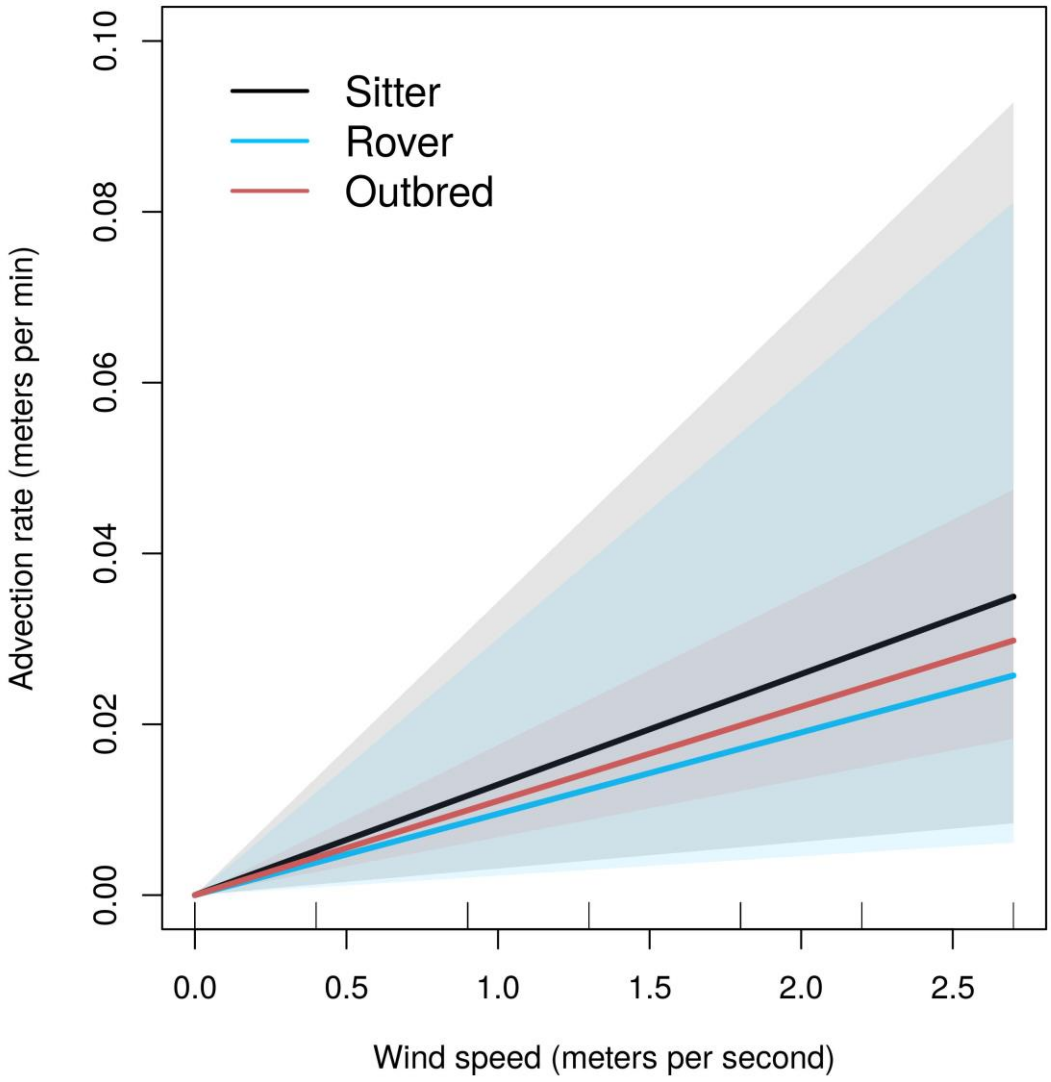

Figure 5.

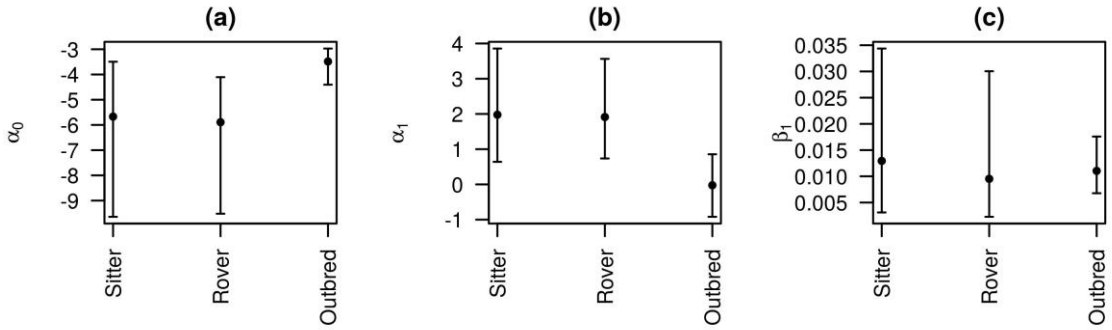

Figure 6.

832 Figure Captions

833

834 **Figure 1**: (a) The experimental field looking towards the South-West towards Blair Road, Cambridge,
835 ON, Canada. The site is lined by trees on all four sides. (b) Depicting the arrangement of sampling
836 points within the experimental field (blue dots). Values on the X and Y-axes represent arbitrary
837 coordinates within a 27 x 27 matrix with coordinate (0,0) representing the centre. The dotted lines
838 radiating out from the centre represent 16 compass directions corresponding to slices where wind
839 directions were obtained (cardinal directions are not specified on this diagram). The red polygon
840 represents the outline of the 21 x 21 matrix that was measured in the field (see red polygon in c). The
841 position of the centre is off-set to increase sampling density in the direction of prevailing winds (see
842 text for more information). (c) Aerial image showing the outline of the experimental field. Each red
843 line along the square depicts the outer trap lines of each side of the sampling grid. The black and red
844 place markers along the red diagonal represent the central release location (e.g. coordinate 0,0) and the
845 weather station that was used to record weather parameters every 15 minutes respectively. (d) Diagram
846 of the traps installed at sample locations. Fly not drawn to scale. See text for more detailed description.

847

848 **Figure 2**: Starting from the top of the panel to the bottom we show time series of fly captures across
849 the experimental field. Each square represents a time unique sequence. t=0.5, t=1.5, t=21, t=26, t=45
850 and t=50 represent captures at 30 minutes, 1.5 hr, 21 hrs, 26 hrs, 45 hrs and 50 hrs after release of the
851 flies respectively. The left set of panels represent the time series for sitter (for^{S}) flies and the middle and
852 right set of panels represent the time series for rover (for^{R}) and outbred flies respectively. The
853 abundance of flies at each sample location are indicated by unique colour coding. Dark blue areas, as
854 indicated by the draped legend on the right, indicate samples with zero fly captures and areas with
855 darkest red indicate samples with abundances of maximum 300 flies. The gray area within each square
856 indicate locations that did not contain traps.

857 **Figure 3**: Temperature (a) and wind speed (b) and wind direction (c) measured every 15 minute (y-
858 axes) over the 50 hours after release (x-axes). Each dot represents a temperature/wind speed/wind
859 direction measurement, blue dots were measured during daylight and black dots represent
860 measurements after daylight. The green vertical dashed lines in (a) (b) and (c) represent the temperature
861 and wind measurements during the six sampling time points.

862

863 **Figure 4**: The relationship between temperature (x-axis) and the rate of movement (y-axis) for each fly
864 strain. Each fly strain is represented by a bold line (blue = rovers, for^R, black = sitters, for^s and red =
865 outbred flies). The correspondingly coloured shaded areas surrounding each bold line represents the
866 95 % credible intervals for each fly strain. The thin vertical lines at the bottom of the x-axis indicate the
867 range of temperatures that were measured during the course of this field experiment. At cooler
868 temperatures the outbred strain tended to move faster than the rover and sitter strains, which showed
869 very little movement. At warmer temperatures the diffusion rate of outbred flies remain largely
870 unchanged while rover and sitter diffusion increased (i.e. at temperatures > 18 ^oC).

871

872 **Figure 5**: Depicting the relationship between wind speed (x-axis) and advection rate (y-axis). The
873 advection rate (metres per minute) is positive if flies are dispersing in the direction of wind and
874 negative if flies are dispersing against wind direction. For each fly strain the posterior means are
875 represented by bold lines (blue = rovers, for^R, black = sitters, for^s and red = outbred flies). The
876 correspondingly coloured shaded areas surrounding each bold line represents the 95 % credible
877 intervals for each fly strain. For all three strains the advection rate is positive and increases with wind
878 speed.

879

880 **Figure 6**: Parameter estimates for each fly strain associated with diffusion rate (Eq. 2, panels a and b),
881 advection rate (Eq. 3, panel c. Each black dot represents the posterior mean with 95 % credible interval
882 (vertical whiskers). In panel c positive values indicate the tendency to disperse with wind and negative
883 values indicate the tendency to move against wind direction. The advection parameter is positive for all
884 three fly strains.