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Tracking dispersal across a patchy landscape reveals a dynamic interaction between genotype and habitat structure

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Theoretical and empirical studies often show that within populations, individuals vary in their propensity to disperse. We aspired to understand how this behavioural variation is impacted by the distribution and pattern of food patches across a landscape. In a series of experiments we examined how inter-patch distance and the distribution of food patches influenced dispersal in wild-type strains of *Drosophila melanogaster* with natural allelic variants of the *foraging* (*for*) gene known to influence dispersal in this species. The 'rover' strain was homozygous for the for^R allele (more dispersive) whereas the 'sitter' strain was homozygous for for^s (less dispersive). We also assessed an outbred population of flies with an unknown dispersal propensity. Dispersal was assayed in a multi-patch lab arena (25 cells, 5 × 5 array). In the inter-patch distance trials, landscapes of two different sizes (small versus large) were used, both with food in all 25 cells. Dispersal was reduced in the large landscape relative to the small landscape for all three fly strains. Sitter dispersal was lowest relative to both rovers and the outbred flies, whose dispersal tendencies were similar. In the patch distribution trials, flies were assayed in landscapes with varying distribution and number of cells containing food. Dispersal generally increased as the number of patches with food increased, however, rovers and sitters adopted similar dispersal strategies when food was fixed and limited. Conversely, their strategies differed when the total amount of food increased with the number of patches. We find that both the inter-patch distance and distribution can influence dispersal. However, the effect of inter-patch distance and distribution on dispersals depends on genotype × environment interaction. Our findings highlight the importance of considering G × E when assessing how dispersal strategies and landscape dynamics influence the distribution of animal communities.

Keywords: behaviour, connectivity, dispersal, *Drosophila melanogaster*, food patches, *foraging* gene, habitat structure, habitat tracking, landscape ecology, movement ecology, polymorphism

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Introduction

Dispersal plays a fundamental role in the distribution and persistence of species and communities. In animal systems, short-distance dispersers (dispersal within natal sites) are considered critical to processes that influence adaptation within their home ranges (Gros et al. 2006, Bonte et al. 2010). Short-distance dispersers may also promote biodiversity (Kerr et al. 2002) and mediate community assembly in diverse systems such as coral reefs (Buss and Jackson 1979). Conversely, long-distance dispersers (i.e. dispersal among distant sites) influence gene flow among populations (Hanski and Gilpin 1991) and are considered important for processes such as the rate of spread of pathogens and invasiveness of species (Kot et al. 1996). Long-distance dispersers can also mediate the impact of habitat fragmentation on communities in human-impacted landscapes (With and King 1999, (Hanski and Mononen 2011, Edelsparre et al. 2018). For example, in fragmented landscapes, the interplay between dispersal and habitat structure can determine colonizations and extinctions of sub-populations (Hanski et al. 2017). Long-distance dispersers appear to contribute disproportionally to maintaining genetic variation in response to habitat loss (DiLeo et al. 2018) and this may in turn influence the evolution of dispersal (Masier and Bonte 2020).

In general, animals disperse and forage in environments where food, mates and other resources are irregularly distributed in space and time (Fahrig and Merriam 1985). To meet such challenges, individuals must employ strategies that allow them to best track resources that are critical to their survival, reproduction and ultimately Darwinian fitness (Nathan et al. 2008). Polymorphic movement strategies have evolved within several species, likely in response to irregularities in resource distribution. For example, in planthoppers, mate availability (Denno et al. 1991) and habitat persistence influence the frequency of non-dispersive (wingless) and dispersive (winged) forms (Zera and Denno 1997). In both marine (Schmitt 1996) and freshwater snails (Chase et al. 2001), a tradeoff between resource use and encounter rate has resulted in a dimorphism in which some individuals intensely exploit local resources and capitalize on foraging within a patch while others tend to explore novel resources capitalizing on foraging between patches. Similar polymorphic movement strategies are found in fishes (Grant and Noakes 1987), mice (Kotler and Brown 1988), predatory mites (van Baalen and Sabelis 1995) as well as larval and adult *Drosophila melanogaster* (Sokolowski 1980, Pereira and Sokolowski 1993, Hughson et al. 2018). For most species, the proximal mechanisms that give rise to the behaviour polymorphisms remain elusive; however, the differences in behaviour are thought to be associated with the patchiness of the habitat structure (Armstrong and McGee 1980, Chace et al. 2001, Gloria-Soria and Azevedo 2008). Although some of these behaviours are associated with foraging, they play an important role in movement strategies that differentially track resources in the landscape and as such may have consequences for the spatial distribution and genetic mixing of individuals (Fraser et al. 2001, Ronce 2007). We investigated the interaction between individual dispersal/foraging behaviour and habitat structure in an attempt to offer critical insights into factors that govern connectivity in heterogeneous landscapes. By connectivity, we mean the ability of a landscape to impede and/or facilitate dispersal among habitat patches (Fahrig and Merriam 1985). This is also often referred to as structural connectivity, while the behavioural interaction with landscape structure is referred to as functional connectivity (Tishendorf and Fahrig 2000).

Elucidating the factors that regulate functional connectivity (e.g. foraging, dispersal, etc.) in landscapes is a valuable endeavour. Firstly, factors that influence functional connectivity may provide critical insights into how pattern (habitat structure) and process (dispersal) are related (Fahrig and Merriam 1985). Attempts to gain such insights are particularly challenging (Schumaker 1996, Saura and Martínez-Millán 2001) and, as a consequence, landscape metrics that attempt to capture habitat structure with a single or few indices are often only weakly correlated with dispersal (Schumaker 1996, With and King 1999, Li and Wu 2004, but see Hanski et al. 2017). Common-garden experiments that investigate aspects of habitat structure in isolation may lead to improved landscape indices and consequently to a better understanding of the link between pattern and process. Secondly, elucidating factors that regulate functional connectivity may provide critical insights into the dynamics relating habitat structure to the maintenance of multiple dispersal strategies within and among populations (Bonte et al. 2010, Masier and Bonte 2020). These investigations may, in turn, have implications for understanding how structural connectivity can facilitate or impede the colonization or range expansion of novel environments by individuals that differentially influence these processes (Fahrig and Merriam 1985, Hanski and Ovaskainen 2000, Cote et al. 2017, DiLeo et al. 2018).

The purpose of this study is to examine how fruit flies, *Drosophila melanogaster*, with different dispersal propensities (Edelsparre et al. 2014, Edelsparre et al. 2018) interact with habitat structure (e.g. the distribution and pattern of food patches). In our study, we interpret dispersal in its simplest form defined as any movement with potential for genetic mixing (Ronce 2007). Our experience is that there is neither a distinct dispersal stage nor behaviour that one can safely define as dispersal in fruit flies and many invertebrates (Benton and Bowler 2012). Therefore, any movement resulting in net-displacement we perceive as dispersal. This fits well with how we define dispersal in general and how we measure dispersal in our experiments. There are several ways in which individuals with different dispersal propensities can respond to changes in habitat structure. For example, one possibility is that changes in habitat structure may differentially impact individuals with different dispersal propensities. Under this possibility, less dispersive individuals would be more impacted by changes to habitat structure that reduce connectivity in the landscape than more dispersive individuals. A second possibility is that individuals with different dispersal

propensities may respond in similar ways under some scenarios of habitat structure (e.g. high connectivity landscapes), but differently under other scenarios (e.g. low connectivity landscapes). There are also several ways in which habitat can vary in terms of food patches. For example, habitat can vary in terms of the turnover rate (Winker et al. 1995), quality (Hanski et al. 2017), distance (Hanski and Ovaskainen 2000) and number and size of patches (O'Neill et al. 1988, Hanski and Ovaskainen 2000). The *Drosophila* model system we use in the following experiments is ideal for exploring these hypotheses. Edelsparre et al. (2018) used a two-patch experiment to show that there are critical distances at which dispersal between patches is reduced rapidly and that such critical distances differ between individuals with different dispersal predispositions. This suggests that inter-patch distance might mediate functional connectivity in complex landscapes and that this process may depend on the inherent dispersal strategy of individuals. It also is known that several movement-related behaviours differ among individual adult *D. melanogaster* (Kent et al. 2009, Edelsparre et al. 2014). For example, the number of patches visited differs among individuals with different foraging behaviours (Anreiter et al. 2017). Taken together, this suggests that 1) distance between and distribution of food patches might play a key role in the dispersal of adult *D. melanogaster* in a benign 'landscape' in the laboratory and that 2) the response to these two factors may differ among strains with less dispersive and more dispersive predispositions. In the following experiments, we attempt to address these two questions by constructing experimental landscapes that mimic habitat with different inter-patch distances and patch distributions. For inter-patch distance experiments, we predict that increasing inter-patch distances within landscapes will severely reduce the dispersal of flies in general independently of the amount of food in the landscape. Similarly, we expect the reduction in dispersal will impact flies with a less dispersive predisposition more than flies with a more dispersive predisposition, even when food patches are abundant. For patch distribution experiments, we predict that the distribution of food-patches independently of the amount of food in a landscape will affect the dispersal of flies in general. We further expect to see differences among more and less dispersive flies when food patches are few, but similar when food patches are abundant. Our predictions are qualitative rather than quantitative because we do not know whether flies respond to patch-structure by dispersing faster/slower or in larger/smaller proportions (or both).

Methods

To examine how flies with different dispersal propensities performed in assays where patch distance and the distribution of patches were varied, we reared two strains of wildtype flies that differed in alleles of the *foraging* gene (de Belle et al. 1993). The more dispersive strain, rover, carries two for^{R} alleles and the less dispersive strain, sitter, carries two for^{s} alleles. Although we are not directly investigating the allelic effects of *for* in these experiments, the allelic effects on dispersal in *Drosophila melanogaster* have been described in Edelsparre et al. (2014, 2018). To examine how a general population performed, we reared an outbred population of flies that originated from Sudbury, Ontario, Canada (collected in 2012 by Thomas Merritt). The outbred population was included for two reasons. First, we were interested in understanding where rover and sitter dispersal would fall relative to an outbred population, and two, including an outbred population in our study, would allow us to evaluate how a general population would respond to changes in patch structure. As such, the rover/sitter strains were used as proxies for individuals with different dispersal strategies and the outbred population allowed us to examine how a population with multiple dispersal strategies respond to changes in the landscape. The outbred population was produced by combining 92 iso-female lines. Currently, we do not know the genetic contribution of *for* in this population, although preliminary analysis on larval path-lengths suggests there are phenotypically more rovers in this population. This still remains to be conclusively tested. The outbred population was produced as follows: approximately 100–150 flies from each iso-female line were randomly assigned to one of six 170-ml sponge-topped plastic *Drosophila* bottles that contained 40 ml of standard fly medium. Overall, we created four bottles each containing 15 different lines and two bottles each containing 16 lines. Prior to the laboratory trials, adults from the six bottles were transferred to population cages and were allowed to interbreed for a single generation in 10 open bottles placed inside the cage. Subsequently, flies were collected from bottles in a haphazard order prior to experimental trials. All flies, including the rover and sitter strains, were maintained at 23°C (± 2) with a 12/12-h light/dark cycle with lights on at 06:00 h. Flies were 6–8 days post-eclosion at the commencement of each trial.

We examined the role of the distance between and the distribution of food patches in a general multi-patch dispersal assay. To do this, we constructed a dispersal arena that consisted of 25 cells (4.8 cm high and 2.9 cm wide) connected by clear plastic tubing (diameter 6.4 mm) in a 5 × 5 cells array (Fig. 1). Arranging cells in an array allowed us to manipulate the location of food patches while always using the centre cell (the release site) as the point from which dispersal could be assessed for all flies. This provided flies with a choice between remaining on a 'familiar' patch or disperse throughout an unknown landscape. Flies could achieve flight within cells, however, the only mode of dispersing among patches was by walking. Although flies in nature disperse primarily via flight, or a combination of flight and walking, our aim was to assay flies' relative willingness/reluctance to disperse throughout an unknown landscape rather than assaying absolute dispersal distances or dispersal endpoints. The relative willingness/reluctance to disperse into an unknown environment we assume to be similar regardless of the mode of transportation and our previous work has shown that walk-based dispersal assays are correlated with dispersal in the field and not affected by differences in walking ability/capacity

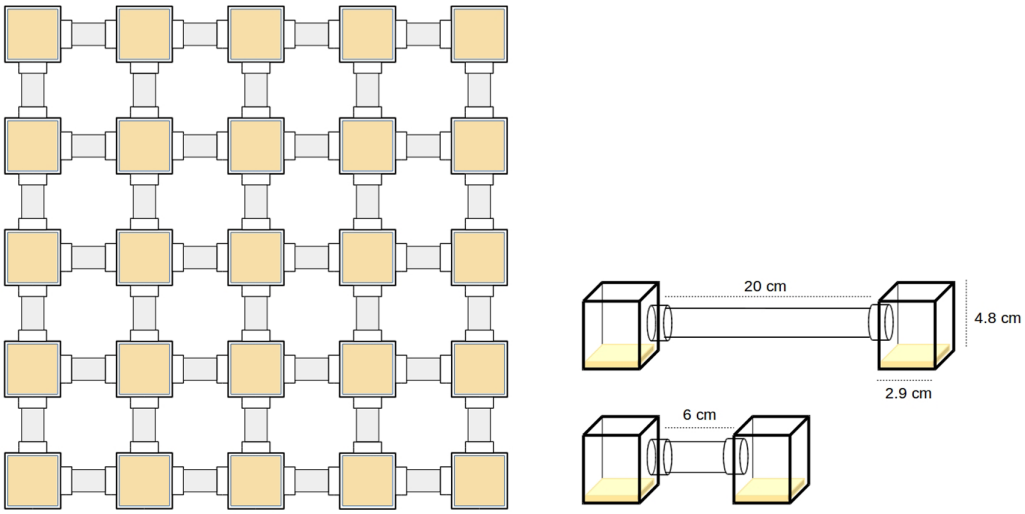

Figure 1. Schematic representing the general multi-patch dispersal arena (left panel) and the different lengths of tubing (right panel) used for the distance trials. In the left panel, the entire square represents a top view of the arena, with each cube representing a cell with food (yellow squares). The white narrow rectangles attached to each cell represent connectors that connected the tubing (gray rectangles) that facilitated dispersal between cells. In the right panel, each square represents a cell containing food (yellow) and the horizontal lines represent the tubing that connected each cell in the dispersal arena. The top diagram represents tubing of 20 cm that connected cells in the largest dispersal arena (100 × 100 cm) and the bottom diagram represents tubing of 6 cm that connected cells in the smallest dispersal arena (40 × 40 cm).

(Edelsparre et al. 2014). Thus, fly movement throughout the landscape was assumed to reflect their dispersal propensity and this operational definition fits well with our definition of dispersal in general (Ronce 2007).

The effects of the distances between and the distribution of food patches were examined in two sets of experiments. The distance effect was assayed in arenas of two different sizes (Fig. 1). In the small arena, cells were connected by 6-cm long tubing, such that the entire arena measured approximately 40 × 40 cm from corner to corner with an inter-cell distance of 8.9 cm. In the large arena, cells were connected by 20-cm long tubing and measured approximately 100 × 100 cm from corner to corner with an inter-cell distance of 22.9 cm (Fig. 1). These distances were chosen because previous findings demonstrated that sitter dispersal was reduced rapidly between 40 cm and 80 cm in a simple two-patch arena whereas rover dispersal remained unchanged across both distances (Edelsparre et al. 2018). Therefore, at the landscape level, the small and large arenas were expected to impose a 'challenge' to both sitter and rover dispersal because together they cover a critical distance (Edelsparre et al. 2018) for at least one of our strains (i.e. sitters) while still providing connectivity via smaller inter-cell distances within each arena. We use the term challenge because any changes in movement in response to distance likely involve a behavioural change in the willingness/reluctance to move from one patch to another based on how challenging flies perceive a given distance. However, we never formally quantified behavioural or physiological costs related to increased dispersal distances. For the distance trials, food was placed in every cell such that each dispersal arena contained 25 food patches. Additionally, each food patch consisted of 2 ml yeast-sugar-agar medium that was prepared 24 h prior to each trial. The yeast–sugar–agar medium was prepared by mixing sugar with dead yeast and agar. For 1 l of medium 100 g of sugar was mixed with 100 g of yeast and 17.43 g of agar in 1 ml of tap water. Eight g of $C_4H_4KNaO_6$, 1 g of KH_2PO_4 and 0.5 g each of NaCl, $MgCl_2$, $CaCl_2$ and $Fe_2(SO_4)_3$ was added and the entire mixture was autoclaved.

The patch distribution trials were conducted using the small 40 × 40 cm dispersal arena using four different 'landscape' treatments (Fig. 2). We used the small arena for these experiments to ensure movement throughout the landscapes, and consequently obtain sufficient data for the analysis. The first two landscape treatments consisted of five food patches, the first had all five patches clumped together (clumped landscape) whereas the second had five patches scattered (scattered landscape) between the central and the four corner cells (Fig. 2). The remaining two landscape types consisted of a 9-patch and a 25-patch landscape (Fig. 2). The patch distribution trials were divided into two parts. First, dispersal was assayed in landscapes with increasing patch density where the total amount of food in the assay was fixed according to the amount of food in the 5-patch arena; the amount of food per patch in the 9 and 25-patch landscapes was diluted accordingly. Second, dispersal was assayed in landscapes with increasing patch density where each food patch consisted of 2 ml of growth medium as described above. In this case, the total amount of food increased with the number of patches such that dispersal arenas consisting of 5, 9 and 25 food patches contained 10, 18 and 50 ml of total food, respectively. All food patches contained 2 ml of medium, irrespective of landscape type and level of dilution.

For both the patch distance and the patch distribution trials, dispersal was assayed separately for rovers and sitters. An

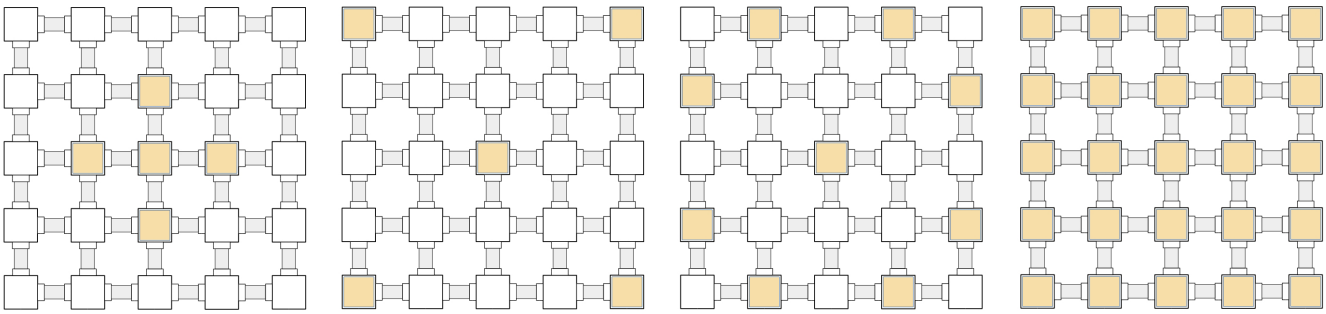

Figure 2. Schematic illustrating the four landscape types used in the distribution trials. Cells with food are depicted in yellow and empty cells are depicted in white. From left to right: landscape types with 5 (clumped and scattered), 9 and 25 food patches, respectively. In one half of the trials the total amount of food was fixed by diluting the food patches in the 9 and 25 landscape types such that all landscapes contained a total amount of food equivalent to a landscape with 5 food patches. In the second half of the trials, the total amount of food increased with the number of patches in the landscape; the 5, 9 and 25 landscape types contained 10, 18 and 50 ml food respectively (see text for full description).

experimental trial involved briefly anesthetizing 25 males and 25 females of each strain with a mild dose of CO_2 to help facilitate their transfer into the central cell of the arena. We chose a density of 50 flies because we had previously assayed dispersal in groups of 64, 32, 16, 8 and single flies and consistently found rover/sitter differences (Edelsparre et al. 2014, unpubl.). In these trials, male and female flies were assayed together, and during the trials we did not distinguish between the sexes. Flies were permitted 5 min to recover from CO_2 anesthesia. The time required for recovery did not differ between strains. Upon recovery, flies were able to freely disperse throughout the arena. Dispersal was determined by counting the number of flies in each cell every 20 min for 8 h. This resulted in a time series that consisted of 24 intervals (including time zero). Preliminary experiments using the small arena with 25 food patches suggested that intervals of 20-min provided the optimal time interval for observing transitions between food patches. Landscape type (5 clumped, 5 scattered, 9 and 25 food patches) and treatment (fixed and increasing total amount of food) were randomized for each trial day to avoid sequential effects, however, rovers and sitters were always assayed simultaneously in the same landscape type and treatment to ensure identical ambient environmental conditions on any given trial day. Five replicate trials were run for each landscape type for each of the three fly strains for each of the distance and patch distribution trials. In all trials, none of the food patches were depleted and eggs were found in all types of landscape regardless of the quality of the food.

Analysis

Dispersal for each treatment was quantified by estimating the total number of movements for each time interval across each arena. This was done by determining the number of flies that changed cell location (i.e. transitions) and summing those transitions across a given arena for each time interval. This provided a time series of the total number of transitions within a given arena for each 20-min observation. The transitions thus represented our proxy for dispersal over time. We did not include density in individual cells in our analysis for two reasons. Firstly, we did not consider 50 flies a high density, and secondly, our level of replication was at the landscape level rather than at the patch-level.

To explore how flies with different dispersal strategies interact with landscape type, we used locally weighted regression to identify how each strain tracked landscape type over time. Because our predictions are qualitative rather than quantitative identifying trends over time required training a model on time-series data. Locally weighted regression is suitable for identifying trends in time series data and is particularly useful for data where observations may be auto-correlated (Cleveland and Devlin 1988). For both the distance and patch distribution trials, we further extracted the predicted transitions over time for rovers and sitters to compare how more dispersive (rovers) and less dispersive (sitters) flies tracked changes in the landscapes. These predictive models plotted rovers and sitters together to directly compare their performance in all landscape types. To determine statistical differences between the response of rovers and sitters to each landscape treatment we estimated the 95% confidence interval around the fitted regression lines and visually determined whether intervals overlapped. Combining regression estimates with confidence intervals provides a strong approach to detect treatment differences (Nakagawa and Cuthill 2007). All statistical analyses were conducted with R (ver. 3.3.3, <www.r-project.org>) and using the package ggplot2 (Wickham 2016) to produce the figures. In all figures the data points are jittered for visualization purposes.

Results

Patch distance trials

There was a clear effect of distance on the movement of all three strains of flies. Irrespective of strain, flies were dispersing earlier in the small arena (inter-cell distance was 8.9 cm) compared to the large arena (inter-cell distance was 22.9 cm;

compare top with bottom panels in Fig. 3). Additionally, the number of transitions decreased in the large arena compared to the small arena. Although rovers dispersed earlier and had a higher number of transitions than sitters in the small and large arenas the strain effect was more pronounced in the large arena. Sitter dispersal was almost negligible in the small arena (bottom panel in Fig. 3). The outbred strain dispersed the earliest of all three strains and had a higher number of transitions in the small arena (top panel in Fig. 3), but in the large arena, the number of transitions of the outbred strain across time was comparable to rovers, but not to sitters (bottom panel in Fig. 3). Figure 4 compares model predictions from the regression smooth among rovers and sitters in the small and large arena.

Patch distribution trials

The dispersal behaviour of rovers, sitters and outbred flies depended on the total amount of food in the landscape. When the total amount of food in the landscape increased with the number of patches, both rovers and sitters increased the number of transitions in landscape types with nine food

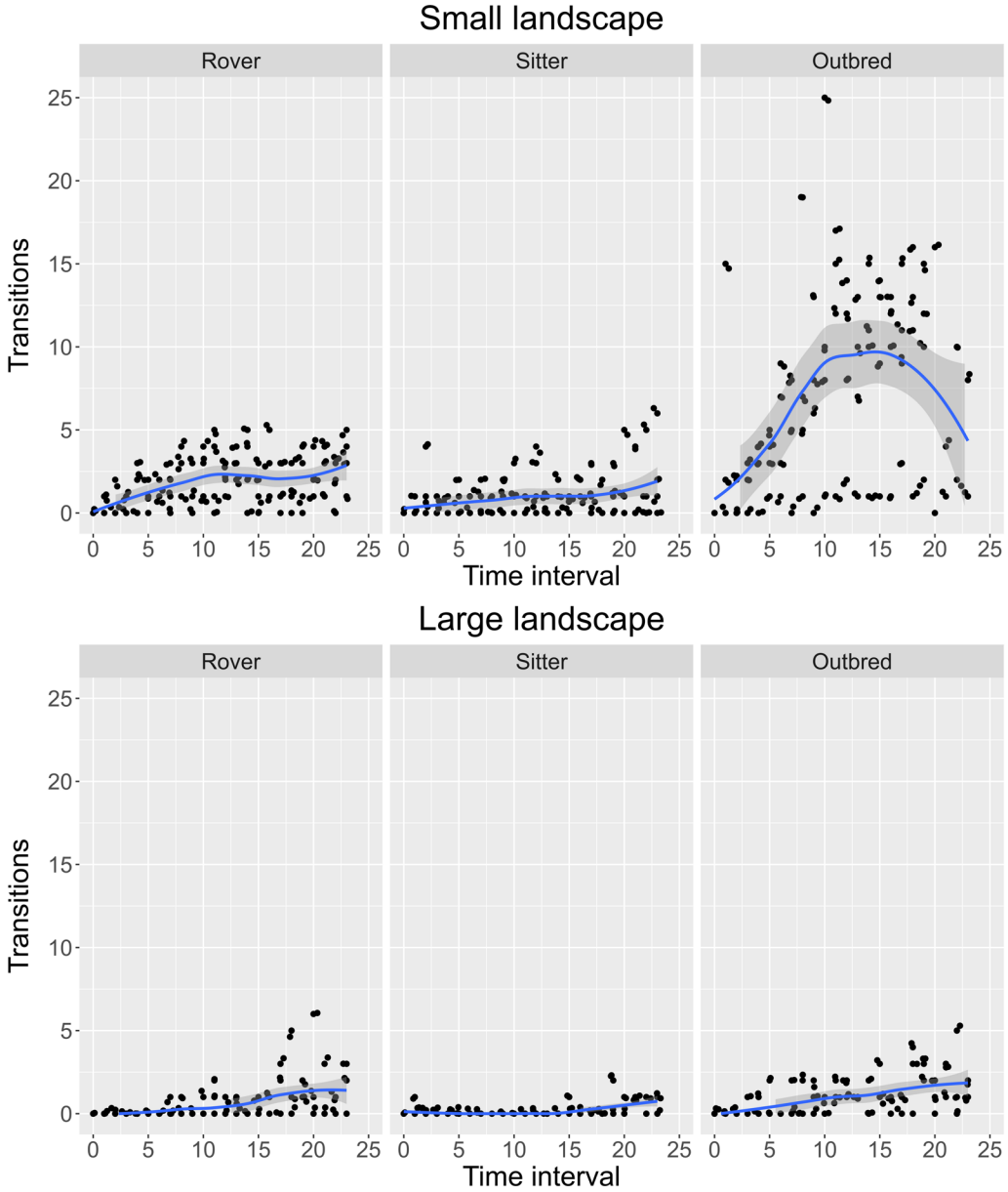

Figure 3. Patch distance trials. The number of transitions (y-axis) over time (x-axis) for rovers (left panels), sitters (middle panels) and outbred strain (right panels) in the small (top panels) and large (bottom panels) dispersal arena. Each black point represents the total number of transitions for a given trial at a given time, each bold blue line represents the locally weighted regression line and the gray shaded areas represent the 95% confidence intervals. Five replicate trials were run for each strain.

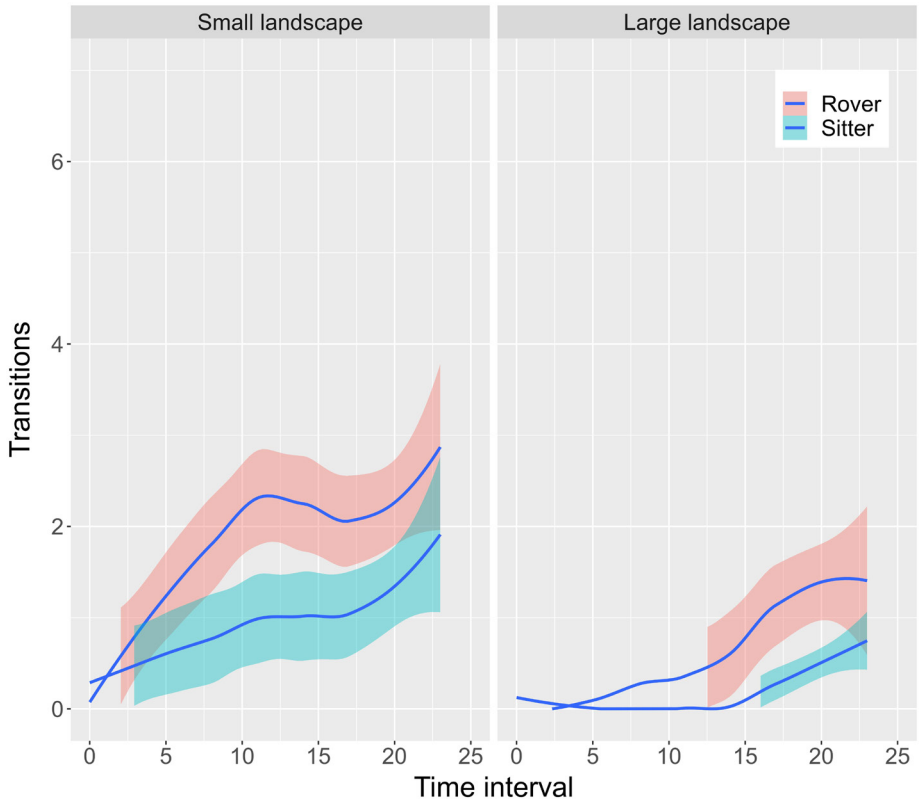

Figure 4. Comparing model predictions of the number of transitions (y-axis) over time (x-axis) for rovers (blue bold line with red shading) and sitters (blue bold line with blue shading) in the small arena (left panel) and the large arena (right panel). The red and blue shaded areas represent the 95% confidence interval of rovers and sitters respectively. Model predictions are based on the locally weighted regression of the empirical data displayed in Fig. 3.

patches more than in landscapes with 5 and 25 food patches (Fig. 5, 6). Under these conditions, the outbred flies had the highest number of transitions in the landscape with 25 patches whereas the number of transitions over time was comparable in landscapes with five and nine patches for this strain (Fig. 7). When the total amount of food was fixed across all landscapes rovers and sitters and outbred flies increased their transitions over time in the 25-patch landscape relative to landscapes with either five or nine patches (Fig. 5–7). The number of transitions increased for rovers and sitters when five food patches were scattered compared to when five food patches were clumped (Fig. 5, 6). This was also the case for the outbred strain (Fig. 7).

Comparing rover/sitter response to fixed and increasing total amount of food in the patch distribution trials

The predictive models from the locally weighted regression showed that when food is fixed across all three landscape types (Fig. 8) rovers and sitters exhibited a similar response to increasing number of patches; transitions increased with patch number for both rovers and sitters and there were no detectable differences among strains (95% CI's overlap) in all four landscapes. However, when the total amount of food increased with the number of patches, the response to landscapes with 9 and 25 patches differed between rovers and sitters (Fig. 9). This difference was due to rovers increasing the total number of transitions across both landscape types compared to sitters and the increase in transitions in rovers occurred significantly earlier post-release compared to sitters. (Fig. 9). In landscapes with 25 food patches, both rovers and sitters decreased the total number of transitions over time when the total amount of food was high (50 ml) compared to when the total amount of food was fixed (10 ml) (compare right panels in Fig. 8, 9). The number of transitions among rovers and sitters were remarkably similar for the landscapes with five scattered and nine diluted food patches (Fig. 10). A landscape with five scattered patches and one with nine diluted patches thus produced a similar dispersal pattern for both rovers and sitters.

Discussion

Investigating how polymorphic dispersal strategies interact with the distance between patches and with the distribution of food patches yielded a number of key results. First, the distance between food patches in a multi-patch laboratory arena played a critical role in determining 'landscape' connectivity

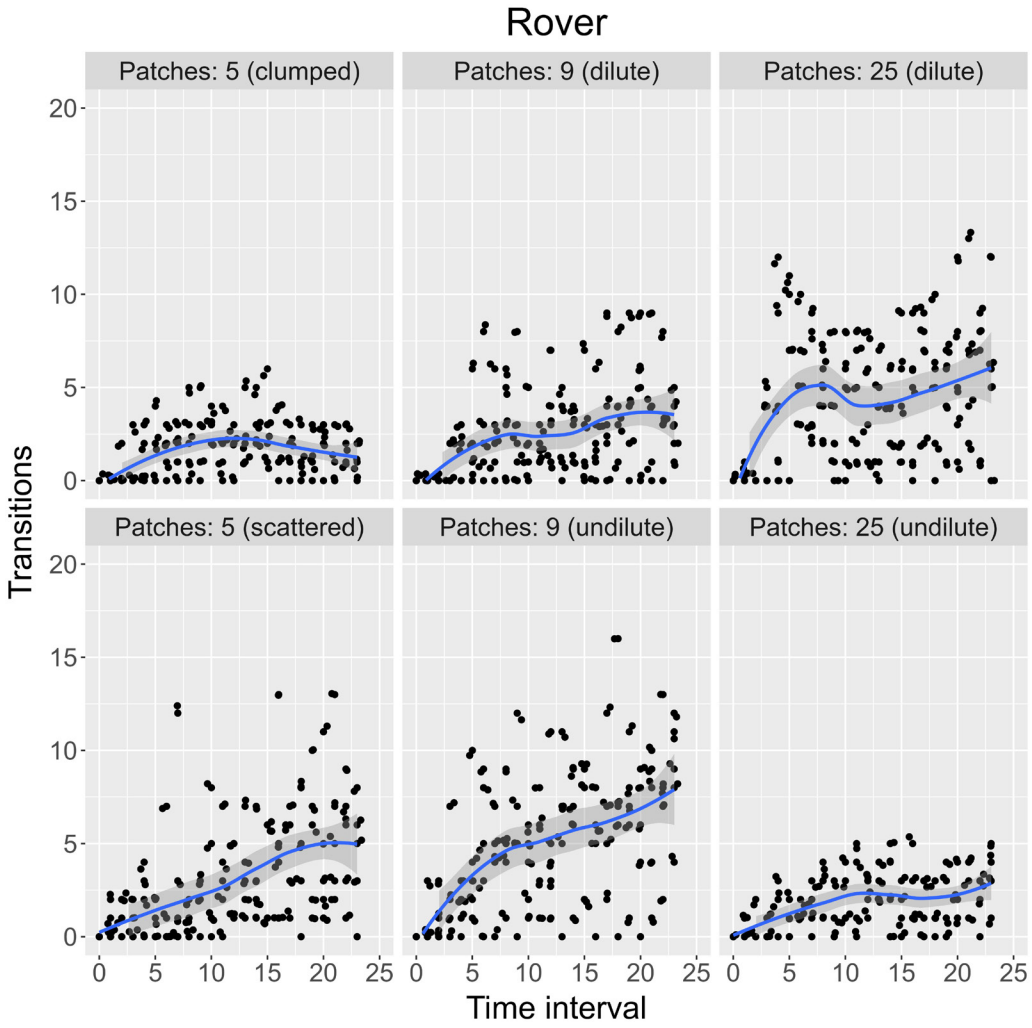

Figure 5. Patch distribution trials. The number of transitions (y-axis) over time (x-axis) for the rover strain in landscape types with 5 (left panels), 9 (middle panels) and 25 food patches (right panels). Each black point represents the total number of transitions for a given trial at a given time, each bold blue line represents the locally weighted regression line and the gray shaded areas represent the 95 percent confidence intervals. The top three panels represent the treatment where the total amount of food was fixed despite changes in the number of food patches (5 clumped; 9 dilute; 25 dilute) and the three bottom panels represent the treatment where the total amount of food increased with the number of food patches (5 scattered; 9 undilute; 25 undilute). Five replicate trials were run for each landscape type in both treatments.

both for flies with a less dispersive and a more dispersive dispersal strategy. This conclusion is based on the finding that both rover (more dispersive) and sitter (less dispersive) dispersal was reduced substantially when the distance between patches in the landscape was increased from a small to a large arena. In the large arena, the reduction was most pronounced for sitters while the reduction in dispersal for the outbred strain mirrored that of rovers. This suggests that in multi-patch landscapes with abundant, and homogeneously distributed food patches, increasing the distance between patches beyond a certain distance can cause a significant reduction in dispersal for one population of flies (sitters), but less so for another population of flies (rovers and outbred). Second, when 'landscape' size was fixed (i.e. small landscape) the distribution of food patches within the landscape also played a key role in determining connectivity. Dispersal increased with increasing patch density and this effect was similar for each strain, suggesting that when food in the landscape was fixed and limited the flies adopted similar dispersal strategies. Conversely, when the total amount of food increased with patch density, rovers, sitters and the outbred strain adopted different strategies. Rovers increased dispersal in landscapes with 9 and 25 food patches compared to sitters. In addition, both rovers and sitters increased dispersal rates in landscapes with 25 food patches when the total amount of food was limited (5 ml) compared to when the concentration of food in the landscape was high (50 ml). Consequently, drivers for dispersal may be low when competition for food is reduced. This further suggests that flies, in general, may increase dispersal in low-quality landscapes (DiLeo et al. 2018). Interestingly,

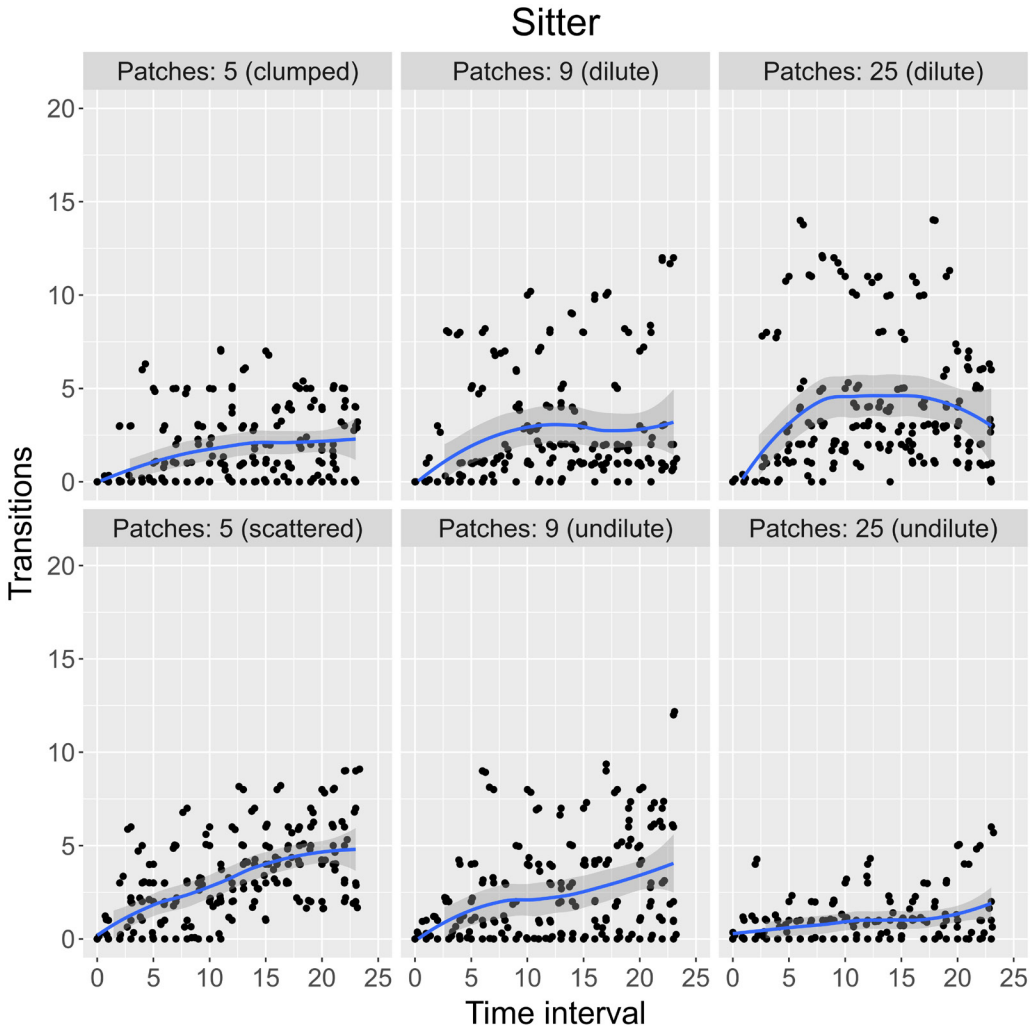

Figure 6. Patch distribution trials. The number of transitions (y-axis) over time (x-axis) for the sitter strain in landscape types with 5 (left panels), 9 (middle panels) and 25 food patches (right panels). Each black point represents the total number of transitions for a given trial at a given time, each bold blue line represents the locally weighted regression line and the gray shaded areas represents the 95 percent confidence intervals. The top three panels represent the treatment where the total amount of food was fixed despite changes in the number of food patches (5 clumped; 9 dilute; 25 dilute). The bottom three panels represent the treatment with the total amount of food increasing with the number of food patches (5 scattered; 9 undilute; 25 undilute). Five replicate trials were run for each landscape type in both treatments.

the dispersal of rovers and sitters depended on whether landscapes offered clumped or scattered food patches. Both rovers and sitters increased their dispersal rates when five food patches were scattered compared with when the five food patches were clumped in the middle. There is a possibility that we may have underestimated the number of transitions in the clumped landscape. This is because flies in the clumped landscape may have switched places between observations more often than flies in scattered landscapes. However, if our finding regarding clumped and scattered landscapes holds, this suggests that the distribution alone and not the number of food patches can influence how flies track resources in the environment. This is further corroborated by the similarity in dispersal rates observed among rovers and sitters in landscapes with five and nine patches. Both landscapes offered the same total amount of food and patches were scattered towards the four corners of the landscape.

Our finding that both distance and patch distribution influence dispersal is important. In landscape ecology, indices that describe the distribution and number of habitat patches within a landscape are used to understand how landscape connectivity influences dispersal (Fahrig and Merriam 1985, O'Neill et al. 1988, Saura and Martínez-Millán 2001). Our findings suggest that using one, or few, indices to describe landscapes may only weakly incorporate the strength of both patch distance and distribution into dispersal models (Li and Wu 2004, Cote et al. 2017). Examples of indices that successfully incorporate several features of networks of habitat have been developed from metapopulations theory (Hanski and Ovaskainen 2000, Hanski et al. 2017). The spatial

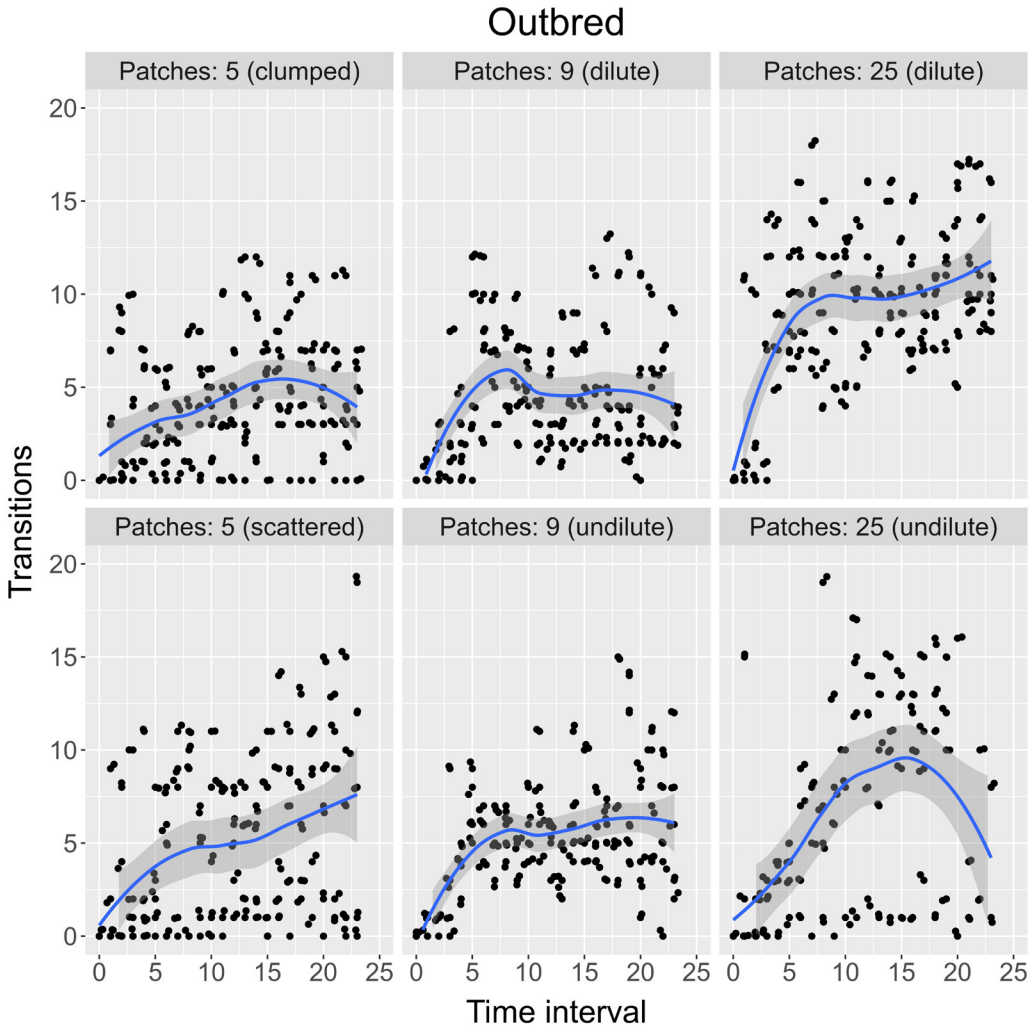

Figure 7. Patch distribution trials. The number of transitions (y-axis) over time (x-axis) for outbred flies in landscape types with 5 (left panels), 9 (middle panels) and 25 food patches (right panel). Each black point represents the total number of transitions for a given trial at a given time, each bold blue line represents the locally weighted regression line and the gray shaded areas represents the 95 percent confidence intervals. The top three panels represent the treatment where the total amount of food was fixed (5 clumped; 9 dilute; 25 dilute) and the three bottom panels to the right represent the treatment where the total amount of food increased with the number of food patches (5 scattered; 9 undilute; 25 undilute). Five replicate trials were run for each landscape type in both treatments.

configuration of habitat captured by such indices successfully links the number and size of habitat patches to colonization and extinction events in sub-populations (Hanski and Ovaskainen 2000). However, the findings from our study suggest that even when food patches are abundant and homogeneously distributed the distance between them can play a critical role in determining dispersal across landscapes (Heino and Hanski 2001). In fact, dispersal can be severely reduced in one part of a population if distances reach a critical point. For example, when distances between patches are beyond the dispersal capacity of a proportion of individuals within a population. Such a critical point is consistent with the notion of a threshold distance beyond which dispersal is rapidly reduced (Gyllenberg and Hanski 1997, With and King 1999, Dytham and Travis 2012, Hanski et al. 2017, Edelsparre et al. 2018). Our findings further demonstrated that even when the distances between patches were fixed in the small arenas the distribution of patches not only determined how the fly strains, in general, tracked the landscape, but also how flies with different dispersal strategies responded to changes in food concentration within landscapes. Taken together our findings suggest that the interaction between patch distance, patch density and dispersal is likely complex. This highlights the importance of considering G × E when assessing connectivity in landscapes. By genotype we mean the complete set of heritable genetic variants in a general sense (Johansen 1903, Saltz et al. 2018). G × E may have implications for the eco-evolutionary dynamics of dispersal in particular (Hanski and Mononen 2011) and genetic diversity in general (Bonte et al. 2018). Consequently, this may exacerbate the difficulty with understanding how structural connectivity influences dispersal when using one or few

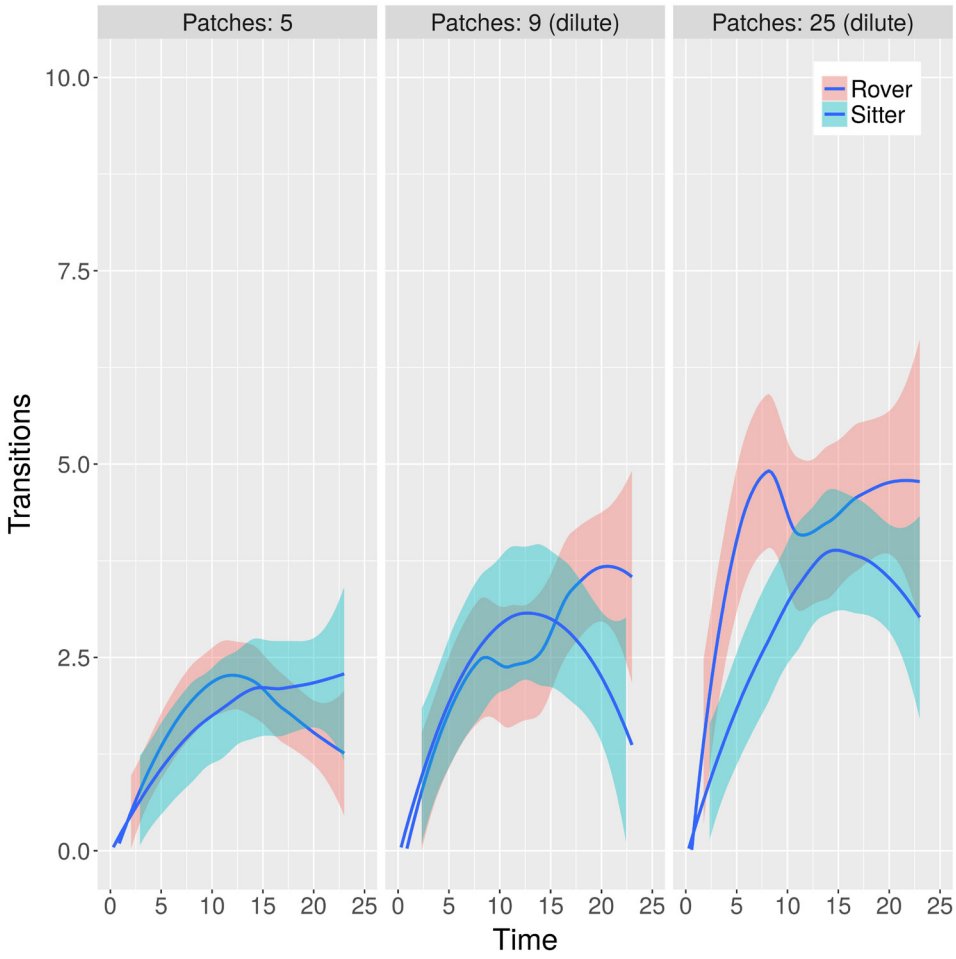

Figure 8. Model predictions of the number of transitions (y-axis) over time (x-axis) for rovers (blue bold line with red shading) and sitters (blue bold line with blue shading) in landscape types with 5 clumped (left panel), 9 (middle panel) and 25 food patches (right panel). Both the red and blue shaded areas represent the 95 percent confidence interval of rovers and sitters respectively. Model predictions are based on empirical data from the patch distribution trials where the total amount of food remained unchanged across all three landscape types.

landscape descriptors. Understanding how landscape factors separately and together dynamically contribute to structural connectivity could inform the development of better landscape descriptors (With and King 1999, Hefley et al. 2017) and in turn improve our understanding of how structural connectivity influences dispersal among populations with multiple dispersal strategies (Hanski and Ovaskainen 2000, Cote et al. 2017, Hanski et al. 2017, DiLeo et al. 2018).

The question of whether individuals within populations track environmental heterogeneity differently is an important one. From an ecological perspective, individuals that track resources over a larger spatial scale may be more important to the colonization of novel habitats and/or range expansion than individuals that track resources over shorter spatial scales (Canestrelli et al. 2016). Similarly, individuals that track resources over a larger scale may be more likely to establish new metapopulations in low connectivity landscapes (Haag et al. 2005, Hanski and Mononen 2011), or reestablish populations following population decline (DiLeo et al. 2018). The findings from this study support this notion. Rovers dispersed at higher rates in both the small and the large arena. Even though both rovers and sitters reduced their dispersal when the distance between patches was large, rovers were more likely to explore new food patches than sitters. In the context of how dispersal may mediate colonization and range expansion, one expectation is that rovers would be more likely to influence these processes relative to sitters and even more so in landscapes where the distance to new food patches increases beyond the dispersal propensity of sitters. This may be the case for butterflies in the Åland islands in Finland where individuals with higher flight-metabolic rates are more likely to colonize new habitat with low connectivity than individuals with lower flight-metabolic rates (Haag et al. 2005). From an evolutionary perspective, within-population differences in tracking environmental heterogeneity could have implications for the evolution of novel traits (Zuk et al. 2014). For example, in eastern Australia, the southward invasion of *Drosophila melanogaster* was not random (reviewed by Hoffmann and Weeks 2007) and this dispersal pattern led to clinal variation in several morphological traits, including

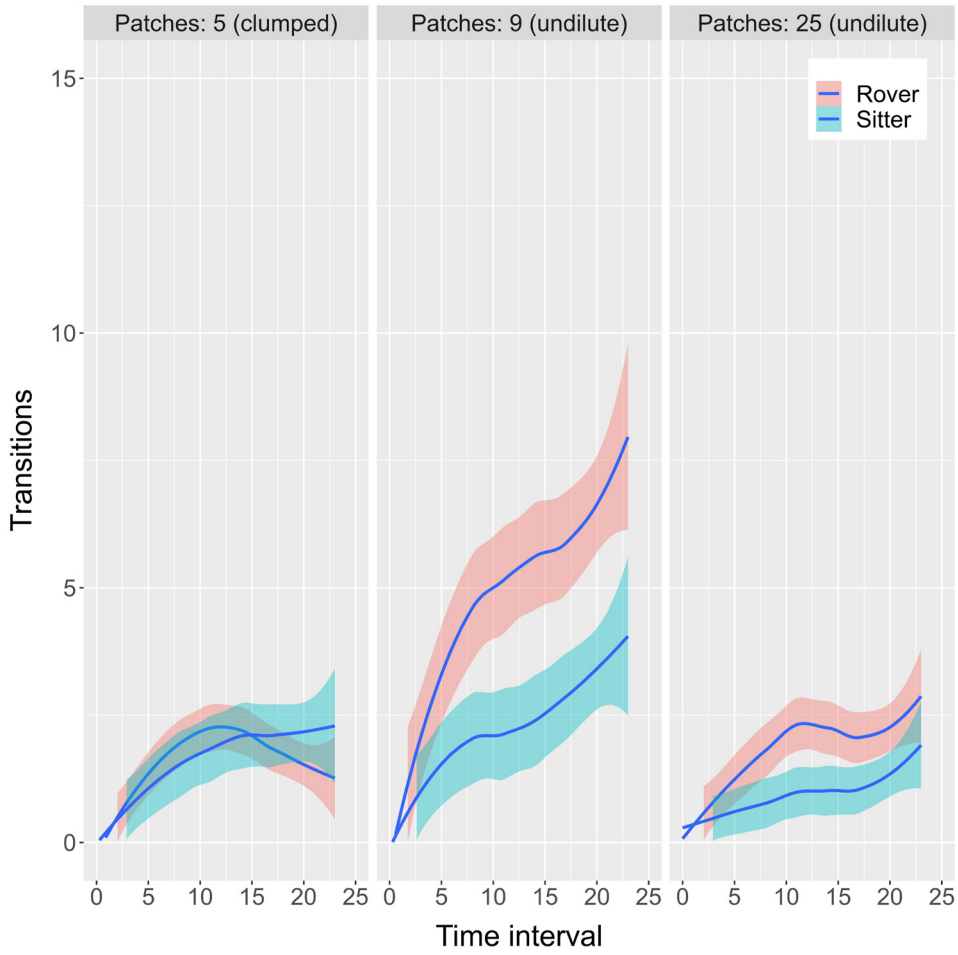

Figure 9. Model predictions of the number of transitions (y-axis) over time (x-axis) for rovers (blue bold line with red shading) and sitters (blue bold line with blue shading) in landscape types with 5 (left panel), 9 (middle panel) and 25 food patches (right panel). Both the red and blue shaded areas represent the 95 percent confidence interval of rovers and sitters respectively. Model predictions are based on empirical data from the treatment trials where the total amount of food increased with the number of patches across the landscape types.

wing (James et al. 1995) and egg size (Azevedo et al. 1996) as well as changes in life-history such as development time (James and Partridge 1995, Weeks et al. 2002) and the timing of egg production (Mitrovski and Hoffman 2001). Interestingly, although to our knowledge no studies currently have investigated allelic variation in *for* in Australian populations, there is clinal variation at the *for* locus in North American *D. melanogaster* (Fabian et al. 2012). Investigations of *for* in Australian populations could have significant implications for understanding how dispersal may have influenced the clinal ecology and evolution of the Australian *D. melanogaster* invasion.

The findings from the present study raise several important questions regarding the relationship between habitat structure and dispersal. Polymorphic behaviours within species have been reported in a diverse range of taxa, including fishes, snails and flies (Sokolowski 1980, Grant and Noakes 1987, Schmitt 1996) and several of these examples have been associated with differences in resource exploitation (Armstrong and McGee 1980, Chace et al. 2001). This could suggest a causal relationship between habitat structure and polymorphic dispersal behaviours. Our findings demonstrated that the distribution of food patches in the landscape induced similar dispersal patterns in rovers and sitters when food is fixed, but different dispersal patterns when the total amount of food increased with the number of patches in the landscape. This suggests that dispersal tendencies can be plastic (Martorell and Martinez-Lopez 2014) and depend on the environmental context (Dahirel et al. 2014, 2017). However, it remains an open question whether habitat structure has played a direct role in the evolution of this ability in *Drosophila*. There are some compelling examples from butterflies (Zheng et al. 2009) and planthoppers (Zera and Denno 1997), which suggest that habitat structure can influence variation in dispersal. More recently, an experiment on mites demonstrated that different dispersal strategies can evolve in direct response to the level of connectivity among habitat patches (Masier and Bonte 2020), however, such examples are rare. Indeed, there is generally very little known about the potential role of habitat structure in

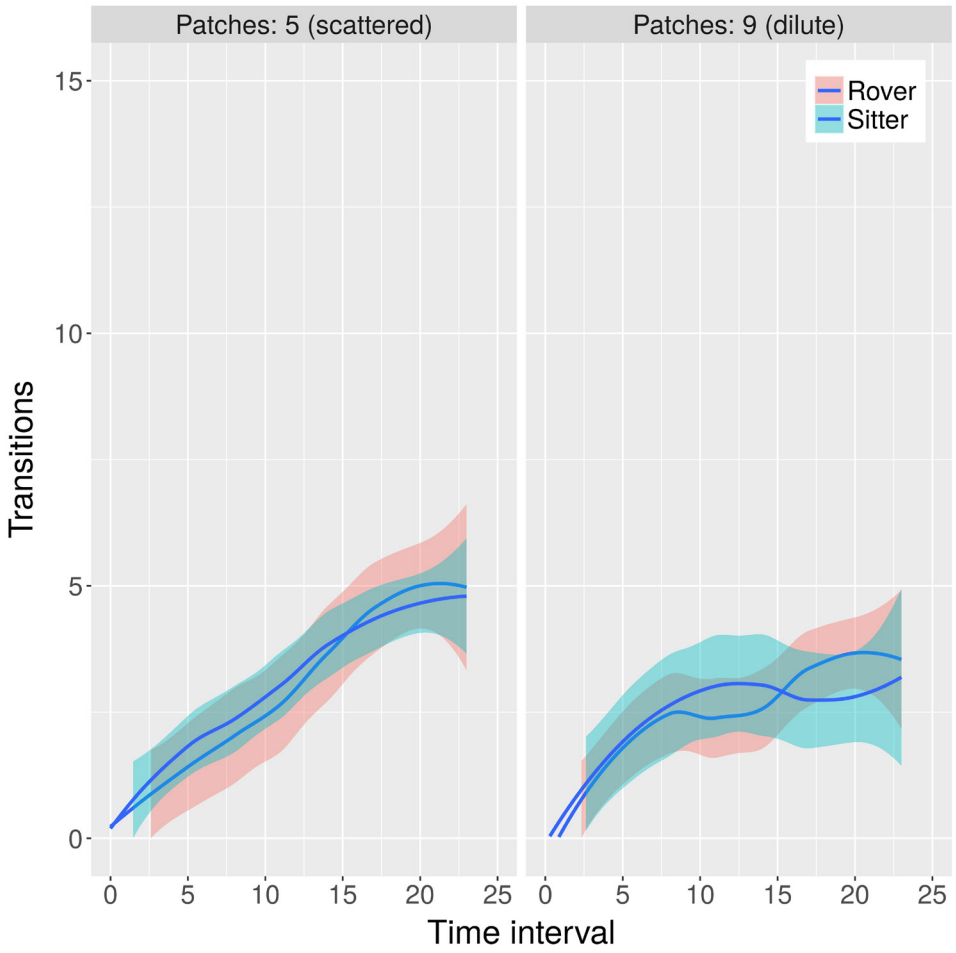

Figure 10. Model predictions of the number of transitions (y-axis) over time (x-axis) for rovers (blue bold line with red shading) and sitters (blue bold line with blue shading) in landscape types with 5 scattered (left panel) and 9 (diluted) food patches (right panel). Both the red and blue shaded areas represent the 95% confidence interval of rovers and sitters respectively. Model predictions are based on empirical data from the trials where both landscapes contain a total amount of food equivalent to a five patch landscape.

promoting and shaping polymorphic dispersal behaviours. This is surprising given that theoretical models suggest that habitat structure plays a critical role in promoting polymorphic dispersal strategies (Bonte et al. 2010, North et al. 2011). In addition, a few studies have shown that organisms can respond to artificial selection on dispersal, including *D. melanogaster* (Tung et al. 2018). More research is needed to better understand conditions under which such behaviours could evolve. A multi-generational study with rovers and sitters allowed to disperse together in arenas similar to the ones used in this study could provide a first step towards such an endeavour. Alternatively, habitat structure may only play a small role in maintaining behavioural polymorphisms. For example, in recently emerged stream brook charr *Salvelinus fontinalis* some individuals are referred to as movers. These individuals prefer prey that is more actively swimming in the middle to the upper water column. Other individuals, stayers, prefer to ambush benthic prey emerging from the sediment (McLaughlin et al. 1994). This suggests that the polymorphism is driven by prey preference and not by differentially tracking the same prey. Lastly, strains of rovers and sitters have been cultured separately in the laboratory for over 30 years in the absence of any larger landscape effects, yet their behavioural differences in foraging activity and dispersal remain (Edelsparre et al. 2014, Anreiter et al. 2017). This suggests at the very least that the cost of maintaining the polymorphism is low, but it does not rule out that habitat structure played a role in the rover/sitter polymorphism at some point. Indeed, laboratory studies on the larval stage of *D. melanogaster* development have shown that density-dependent selection can influence the polymorphism whereas frequency-dependent selection can maintain the rover/sitter polymorphism under limited food availability (Sokolowski et al. 1997, Fitzpatrick et al. 2007). Experiments that vary rover/sitter ratios in each landscape type used in this study and across several generations may be useful to tease apart selection arising from different forces, including selection arising from habitat structure.

Speculations

Although the genetic contribution to dispersal in the outbred population is currently unknown there are several interesting points to notice about this wild population. From the perspective of larval path length phenotype, preliminary trials suggest there were both rover and sitter phenotypes in this Sudbury population (unpubl. results), with rovers in a majority as was the case in the two Toronto populations (Sokolowski 1980, Sokolowski et al. 1997). The majority of the adult dispersal results from the outbred strain reported in the present paper aligned with rover dispersal. However, there were also numerous time intervals with very little dispersal, suggesting a mix of dispersal phenotypes in the outbred population. Overall, the data from the outbred population displayed greater variance and wider confidence intervals than displayed by each of the rover and sitter strains. In addition, some trials in the present study showed that the outbred population appeared to be more dispersive than even rovers (Fig. 3, 7). There are a number of reasons for this finding. For example, one possibility is that more recently wild-caught strains are more robust than lab strains and simply move more. A second possibility is that some selection has occurred in the inbred rover/sitter lines after years of culture in the laboratory, and this is most certainly the case. A third possibility is that there are other alleles of the *foraging* gene as well as other genes in addition to *foraging* that influence dispersal in this population that we do not yet know of (Anreiter and Sokolowski 2019). Finally, a fourth possibility would involve a combination of the ones mentioned above. The outbred population was sampled near its northernmost range in Ontario, Canada, approximately 400 km north of where the original rover and sitter strains were first discovered (Sokolowski 1980). Whether the tendency of this Sudbury population to display increased dispersal is related to its colonization of northern Ontario remains an interesting possibility, although human activity likely contributed to the northward movement of the species. Future work focusing on identifying *foraging* alleles across the Ontario range will provide an important contribution towards understanding the potential role of selection on dispersal phenotypes and underlying genes, including *foraging* in Canadian *D. melanogaster* populations.

In summary, three main conclusions can be drawn from the findings in this study. Firstly, examining the effect of patch distance and distribution revealed clear differences among landscape types and strains. Such effects may otherwise be confounded in metrics that seek to describe the degree to which habitat structure facilitates or impedes dispersal in landscapes. Empirical and theoretical efforts have attempted to bridge the gap between structural and functional connectivity (With and King 1999, Bonte et al. 2010), but with limited success (Schumaker 1996, With and King 1999, but see Masier and Bonte 2020). Combining multiple aspects of landscape structure, including inter-patch distance and distribution, in dynamic models should improve the correlation between landscape descriptors and dispersal (Hefley et al. 2017). Developing dynamic metrics could have implications for managing connectivity within and between habitats that harbour species where dispersal is critical to sustaining healthy gene flow among populations (Opdam 1990, Hanski and Gilpin 1991). Secondly, the findings from this study support the idea that individuals within populations can influence ecological and evolutionary processes disproportionally, depending on how they track environmental heterogeneity. Rovers were generally more likely to explore food patches in both the distance and the patch distribution trials. In the context of dispersal in wild populations of *D. melanogaster*, this could mean that rovers would influence the rate of population spread more so than sitters. This could have implications for colonization or range expansion of novel habitat, particularly in flies and other insects. In turn differential dispersal in novel habitats could have implications for the subsequent evolution of life histories (Mitrovski and Hoffmann 2001, Weeks et al. 2002). Finally, our findings raise important questions regarding the relationship between dispersal and environmental heterogeneity. Although rovers, sitters and outbred flies employed different strategies to track changes in habitat structure there were also instances where changes in the distribution of food patches elicited similar dispersal patterns among the strains. This suggests that rovers and sitters, in particular, maintain behavioural plasticity to accommodate changes in habitat structure. Therefore, endeavours to understand the role of habitat structure in the evolution of polymorphic strategies may, provide critical insights into how landscape connectivity influences the evolution of behavioural differences among individuals. More broadly such endeavours may provide insight into how habitat/dispersal interactions are important to the establishment of novel traits (Zuk et al. 2014, Canestrelli et al. 2016).

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.tdz08kpxr> (Edelsparre et al. 2020).

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Author contributions – AHE conceived and designed the experiments. MJF, MAR and MBA provided significant input that influenced the experimental design. AHE executed the experiments, performed the analyses and wrote the initial draft. All authors contributed substantially to revisions.

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