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Does movement behaviour predict population densities?

A test with 25 butterfly species

Cheryl B. Schultz^{* a}, B. Guy Pe'er^{b,c}, Christine Damiani^d, Leone Brown^e and
Elizabeth E. Crone^f

^a Washington State University, Vancouver, WA, USA

^b Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany

^c German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig,

^d Institute for Wildlife Studies, Arcata, CA, USA

^e University of Georgia, Athens, GA, USA

^f Tufts University, Medford, MA, USA

* Corresponding author: schultzc@wsu.edu

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Summary

1. Diffusion, which approximates a correlated random walk, has been used by ecologists to describe movement, and forms the basis for many theoretical models. However, it is often criticized as too simple a model to describe animal movement in real populations.
2. We test a key prediction of diffusion models, namely, that animals should be more abundant in land cover classes through which they move more slowly. This relationship between density and diffusion has rarely been tested across multiple species within a given landscape.
3. We estimated diffusion rates and corresponding densities of 25 Israeli butterfly species from flight path data and visual surveys. The data were collected across 19 sites in heterogeneous landscapes with four land cover classes: semi-natural habitat, olive groves, wheat fields, and field margins.
4. As expected from theory, species tended to have higher densities in land cover classes through which they moved more slowly and lower densities in land cover classes through which they moved more quickly. Two components of movement (move length and turning angle) were not associated with density, nor was expected net squared displacement. Move time, however, was associated with density, and animals spent more time per move step in areas with higher density.
5. The broad association we document between movement behaviour and density suggests that diffusion is a good first approximation of movement in butterflies. Moreover, our analyses demonstrate that dispersal is not a species-invariant trait, but rather one that depends on landscape context. Thus land cover classes with high diffusion rates are likely to have low densities and be effective conduits for movement.

Key-words Butterflies, correlated random walk, diffusion, dispersal, expected net squared displacement, movement ecology

Introduction

Diffusion is a leading model of animal movement in ecology (Turchin 1998).

Theoretical ecologists use diffusion processes to model animal movement (e.g., Bovet & Benhamou 1988; Holmes *et al.* 1994; Kinezaki, Kawasaki & Shigesada 2010; Ahmed & Petrovskii 2015). Empirical ecologists and conservation biologists use diffusion models to scale up from small-scale measurements to large-scale generalizations about long-distance movement, dispersal and (re)colonization processes (Turchin 1991, Levey *et al.* 2005, Brown and Crone 2016a & 2016b). Diffusion approximates a correlated random walk, so it can be explicitly estimated from animal tracking studies (Kareiva & Shigesada 1983; Schultz 1998), or by embedding correlated random walk (CRW) models into spatially explicit individual based models (e.g., Pe'er *et al.* 2011a; Bennett, Quinn & Zollner 2013; Pauli *et al.* 2013; Bocedi *et al.* 2014; Brown & Crone 2016b; Zalucki, Parry & Zalucki 2015).

The use of diffusion to model animal movement has been widely criticized as too simplistic (Schick *et al.* 2008). This is because animals vary in their movement behaviour based on sex, habitat association, habitat quality, proximity to boundaries or resources, age, propensity to breed, proximity to predators, and numerous other factors (e.g., Gurarie, Andrews & Laidre 2009; McClintock *et al.* 2012; Allema *et al.* 2014; Kallioniemi *et al.* 2014). In addition, diffusion models assume that each move step is independent of the prior step, i.e., they are Markovian (Root & Kareiva 1984), but memory and perceptual abilities in animals make it likely that more complex processes regulate animal movement (Schick *et al.*

2008; Clobert *et al.* 2009; Raghieb, Levin & Kevrekidis 2010; Papastamatiou *et al.* 2011; Fronhofer, Hovestadt & Poethke 2013).

If diffusion is an adequate model of animal movement then slower diffusion rates should lead to higher abundances (Patlak 1953). However, there are reasons why we might not see this relationship in real landscapes. First, it may be that diffusion is an inadequate model of movement, which would make diffusion rates poor metrics for predicting abundance (Turchin 1998). Second, even if diffusion is generally an appropriate model, abundance could primarily be determined by responses to patch edges (Ries & Sisk 2004; Schultz & Crone 2001, Jackson *et al.* 2009) rather than movement within a patch. Third, if the time scales of population (Kinlan, Gaines & Lester 2005; Pinsky *et al.* 2012) or habitat (Hanski 1998) dynamics are similar to those of movement, vital rates and/or metapopulation dynamics, rather than movement, may be the primary predictors of abundance.

To date, several studies have used diffusion rates to predict animal densities (Turchin 1991; Hannunen & Ekbom 2001; Dumont, Himmelman & Robinson 2007; Delgado & Penteriani 2008). Among case studies, seven out of nine species show the qualitative pattern of higher densities in areas with slower estimated diffusion rates (monarch butterflies, *Danaus plexippus*, Zaluki & Kitching 1982; cabbage white butterflies, *Pieris rapae*, Root & Kareiva 1984; ladybugs, *Coccinella septempunctata*, Kareiva & Odell 1987; Anicia checkerspot, *Euphydryas anicia*, Odendaal, Turchin & Stermitz 1989; lygus bugs, *Lygus rugulipennis*, Hannunen & Ekbom 2001; a termite species, *Reticulitermes flavipes*, Puche & Su 2001; and sea urchins, *Strongylocentrotus droebachiensis*, Dumont 2007), and two do not (eagle owls, *Bubo bubo*, Delgado & Penteriani 2008 and another termite species, *Coptotermes formosanus*, Puche & Su 2001). In addition, some studies only use simpler

metrics such as move length, tortuosity, total distance moved, and speed to describe movement (e.g., Skorka *et al.* 2013; Kallioniemi *et al.* 2014; Loos *et al.* 2015), e.g., based on mark-recapture, or radio or satellite telemetry data, such as in Frair *et al.* 2005. These studies often cite the theoretical literature from models based on CRWs or diffusion, but make inferences about animal movement based 1-2 of the aforementioned simple metrics (e.g., move length or distance moved) rather than formal diffusion-based metrics.

Here, we test whether slower movement generally corresponds to higher abundance across 25 butterfly species in four habitat types. We use fine scale behavioural data to make predictions across broad landscape and community scales, extending past the generality of previous studies that generally include only 1-2 species in no more than two habitat types.

In addition, we test whether simpler summary statistics (move length, move time, turning angle, and expected net squared displacement) are sufficient as surrogates of diffusion to predict variation in butterfly densities. Our study differs from past tests of diffusion models in that we ask whether these simple models make statistically significant predictions about abundance across a larger number of land cover classes than past studies, and whether the predictive ability is consistent across multiple species within a taxonomic group.

Materials and methods

Study Area and Environments

We conducted our study at 19 field sites in Israel along a climatic gradient from the arid Negev desert to Mediterranean regions of northern Galilee (Fig. 1a). Each site was located at the intersection of an agricultural field and a semi-natural area. Butterfly densities

and movement behaviours were recorded in four land cover classes: wheat fields, olive groves, semi-natural grasslands or scrublands, and field margins.

The first two land cover classes, wheat fields and olive groves, were common agricultural crop field types that differ greatly in their structure. Wheat fields (Fig. 1b) were open monocultures, most of which were intensively managed with agrochemicals and mechanical disturbance. Olive groves (Fig. 1c) were structurally heterogeneous environments, with rows of mature trees (> 4m height) separated by areas of open habitat, and typically less intensively managed than wheat fields. Butterfly host and nectar plants were patchily found in the open microhabitats of olive groves, and butterflies used the trees for shade, perching or roosting.

The third and fourth land cover classes were the semi-natural grasslands and scrublands outside the agricultural fields (Fig. 1d), and the margins of the fields themselves. The grassland/scrubland areas were open areas containing a diversity of plants not occurring in other areas. Although grazed by goats and cattle, these sites were otherwise undisturbed. The “field margin” land cover class (Fig. 1e) included linear elements such as unpaved roads, fences, or paths that separated agricultural fields from the surrounding semi-natural environment. Field margins were characterized by a heterogeneous mix of vegetation that resulted from elevated nutrient levels, agrochemical use and mechanical disturbances. Ruderal species were often abundant, offering resources including nectar and host plants. The field margin also attracted perching or “ravining” species that establish territories along linear features (Tennent 1995). Field margins ranged in width from 1.5-21 m (average 9.6 m) between sites (for further details see Pe'er *et al.* 2011b).

Butterfly surveys and movement data

We conducted surveys along transects established in sites containing one of the two agricultural field types (olive or wheat), field margin, and the surrounding semi-natural grassland/scrubland area. Each transect consisted of three lines perpendicular to the field margin, starting 50 m within the semi-natural area, traversing the width of the field margin, and extending 100 m into the agricultural field. Transect lines were connected by two 50 m lines parallel to the field margin, one in the semi-natural area and one in the field margin (Fig. 2a, see also Pe'er *et al.* 2011b). Additionally, a 100 m transect was sampled along the length of the field margin. Semi-natural areas were only sampled to a depth of 50 m because the topography in most sites tended to change beyond this depth, rendering the environment no longer homogeneous.

We completed 2-3 surveys along transects at each site from March to May 2006, the peak of butterfly activity in Israel, and the period in which wheat fields and olive groves received minimal treatment. We used standard Pollard Walk methods to conduct surveys between 09:00 and 16:00, under conditions of <50% cloud cover, temperatures of 18-33°C, and wind speeds <10 km/hr. Pollard-Yates indices correlate well with population size in many studies (Thomas 2005; Collier, Mackay & Benkendorff 2008). For each survey, two observers walked at a constant pace of 1 km/hr, searching for butterflies within 5 m of the transect line (i.e., a 10 m wide survey width), and recorded a GPS location for each individual butterfly observed. In addition, we recorded short movement paths for as many butterflies as possible during the surveys. Observer pairs recorded butterfly movement paths from when an individual butterfly was first located, following the butterfly at > 1.5 m distance and registering locations at which the individual landed or changed direction until one of the following conditions was met: 20 seconds, 6 turns, 40 m distance, or the butterfly

disappeared from view. Observer pairs recorded total observation time and resting time of each followed individual. After completion of the observation, one of the two observers recorded the GPS location of each stopping or turning location. We noted land cover class (semi-natural area, field margin, and wheat field or olive grove) for each marked point. When we encountered two butterflies simultaneously, we followed the path of the less common species. For common species, we recorded up to 20 observations per site on a given sampling day. Examples of movement paths are provided in Fig. 2. We conducted our study within a single season because observed differences in diffusion rates between land cover classes are generally much larger than differences between years (e.g. Schultz, Franco & Crone 2012).

Diffusion Rates

We calculated diffusion coefficients (D) for each species \times land cover class combination using the equation $D = \frac{M+2\psi\mu^2}{4\tau(1-\psi)}$, where μ is average move length, M is average squared move length, ψ is mean cosine of the turning angle, and τ is the average duration per move or move time (Turchin 1998, page Box 5.3 and page 102). For each individual, we partitioned the movement path into moves made in each land cover class. Each move consisted of a move length, measured as the distance between turning or stopping points i and $i+1$, and a turning angle θ_i , measured as the angle between move $i-1$ and i . If the movement path contained only two points (i.e., a straight line with no landing behaviours observed), we assigned a very small angle (<1 degree) for the turning angle. This non-zero value was introduced to prevent the calculated diffusion rate from being estimated as infinity (i.e., because a mean turning angle, ψ , of 0 has a mean cosine of 1, reducing the denominator in the above equation for D to 0, and any fraction with a denominator of 0 = infinity). Because flight time was measured for the entire path rather than for each move, we estimated the average speed [meters per second] as $\bar{s} = \frac{\text{total path length}}{\text{total time in flight}}$, and the duration for each move

as $t_i = \frac{l_i}{s} + r_i$, where l_i is the move length preceding stop i and r_i is the resting time at stop i .

We averaged move lengths, move durations, and turn angles over the pooled moves in each species \times land cover class combination (following Schultz and Crone 2001). We estimated diffusion coefficients for combinations for which at least 5 complete moves were recorded, i.e., 5 move lengths, 5 move times, and 4 turn angles. To separate between edge-mediated behaviour and movement behaviour within semi-natural areas, olives groves and wheat fields, we used only data that were collected at least 10 m away from the field margin, i.e., far enough from boundary within semi-natural areas, olives or wheat. The 10 m buffer was based on various studies demonstrating a shift in movement behaviour close to structural habitat boundaries (Haddad 1999; Schultz & Crone 2001; Ovaskainen & Cornell 2003; Ovaskainen 2004; Schultz, Franco & Crone 2012; Zurita *et al.* 2012). We also visually inspected the data to corroborate that this buffer width was consistent with our data. We used all movement behaviour within field margins as this area is, by definition, a boundary-influenced habitat type. For each move within each species \times land cover class combination, we used bootstrapping to create 1000 sample sets of the 4 movement parameters μ , M , τ and ψ . From these we calculated expected net squared displacement, $E(R^2) = \frac{M+2\psi\mu^2}{(1-\psi)}$ for a single move, and diffusion rate, D , for each species \times land cover class across these 1000 sample sets. We based analyses below on the median of bootstrapped estimates of D , $E(R^2)$, μ , τ and ψ .

Density

We used survey data to estimate the density (abundance divided by area) of each species in each land cover class. We estimated abundance for each species at each site using the survey date with the highest count for that species at that site. We calculated the sampling area as the length of the survey transect \times transect width (10 m). We only used density data from each of the four primary land cover classes (semi-natural areas, field margin, olive

groves and wheat fields) and excluded all observations within the 10 m boundary zone for olive groves, wheat fields and semi-natural areas for consistency with the treatment of movement data above.

Statistical Analysis

We determined the relationship between density and diffusion using linear mixed models (lme4 package in R, Bates, Maechler & Walker 2015) with diffusion, wingspan, and diffusion \times wingspan as fixed effects, and butterfly species as a random effect (to account for repeated measures of species, and supported by an initial test of the best model for the random effects structure, Appendix Tables S1a-e, Zuur *et al.* 2009). We did not detect phylogenetic signal in our data (Table S2 and Figure S1), so we did not use phylogenetic regressions because the lme4 package allows greater model flexibility, including the ability to weight models by confidence in the data. We included wingspan estimated to the nearest 0.5 cm using published keys and field guides (Table S3) as an index of body size because it is a potential correlate of density (e.g., Gaston & Lawton 1988) that could influence the relationship between density and diffusion. Because densities may differ among species and among land cover classes, e.g., species for which semi-natural areas whereas versus olive groves are higher quality habitat, we ran an additional analysis with land cover class as a fixed effect in addition to diffusion, wingspan, and diffusion \times wingspan. We used models with land cover as a fixed effect to evaluate the importance of land cover class relative to diffusion for predicting density, and to estimate densities in each habitat type evaluated at median values of wingspan and diffusion. We calculated 95% confidence limits of expected densities by parametric bootstrapping, i.e., taking 0.025 and 0.975 quantiles of 1000 sampled values sampled from a multivariate normal distribution defined by model coefficients and sampling error variance-covariance matrix of fixed estimates (vcov() function in R).

In all models, we log+0.5-transformed diffusion rate and density for each species × land cover class combination to improve normality in the residuals. Because sample sizes were highly variable, with common species having many more movement paths than rare species (Fig. 3), we weighted models by the inverse of the 95% bootstrap confidence interval standardized to a mean of one (to keep the total error degrees of freedom constant). For standardization, we used the confidence interval of the diffusion rate, expected net square displacement, or flight path parameter (μ , ψ , and τ) estimate, as appropriate for the predictor variable in each model.

In addition to testing diffusion as a predictor of density, we tested whether parameters measured directly from flight paths were sufficient predictors of density. For example, does move length sufficiently predict variation in density? We repeated the analyses above with move length, cosine of turning angle and time per move (μ , ψ , and τ , $E(R^2)$, above), in turn, as fixed effects (again with wing span and land cover class as covariates). We log+0.5-transformed move lengths and times per move and logit-transformed cosines of turning angles that were scaled to range from 0 to 1. As a second test of possible independent drivers of density, we quantified the relationships between body size and diffusion, and body size and density, for all species in our data set. Specifically, we calculated median diffusion rate and density for each species. We used linear models to test whether body size was a significant predictor of either diffusion rate or density. This analysis differs from the models above in that we evaluated the relationship among species, averaged across land cover classes, rather than within species, among land cover classes.

Results

We observed a total of 2287 butterflies from 42 species, and recorded 1868 movement paths in 19 sites. After excluding observations at a distance of 10 m from field margins, we obtained a dataset of 1260 movement paths from 40 species. Diffusion rates were calculated for the 25 species among these 40 that had at least 4 complete moves (i.e., included 5 move lengths, 5 move durations, and 4 turn angles) in at least one of the four land cover classes (Fig. 3, Table S1). Sufficient observations to calculate land cover class-specific diffusion rates were available for 22 species in semi-natural areas, 19 species in field margins, 14 species in olive groves and 7 species in wheat fields.

As predicted by general theory, diffusion was associated with density: butterfly densities were higher in land cover types through which they moved more slowly (Table 1, Fig. 4). Neither body size nor the interaction of body size and diffusion were significant predictors of density (fixed effects of wingspan and fixed effects of wingspan \times diffusion, Table 1). When including land cover class in models, diffusion, wingspan and land cover class were strong predictors of density (Table 2), and densities differed significantly among land cover classes (Table 2, Fig. 4). Smaller butterfly species (≤ 30 mm, *Apharitis acamas*, *Freyeria trochylus*, *Pseudophilotes vicrama*, *Satyrrium spini*, *Thymelicus hyrax*, *Thymelicus sylvestris* and *Ypthima asterope*) tended to occur with higher frequency (i.e. high enough frequency to be included in our movement dataset, Fig. 3, Table S3) only in field margins and semi-natural areas and most of the observed species \times land cover class combinations for these species had diffusion rates of < 3 m²/sec. Based on models including diffusion, wingspan, and land cover class as predictors, expected densities were highest in the field margins (median = 24.2 butterflies/ha, CI = 14.5 – 38.8), intermediate in semi-natural areas (median =

10.3 butterflies/ha, CI = 6.5 – 16.3), and lowest in agricultural areas (wheat: median = 2.8 butterflies/ha, CI = 0.9 – 7.5; olive groves: median = 1.7 butterflies/ha, CI = 0.7 – 3.2).

Move length, turning angle and expected net squared displacement were not significant predictors of density (Table 1). Move time, however, was a significant predictor of density with more time per step in areas with higher density (Table 1). Wingspan and the interaction of wingspan with length, time, turning angle and expected net squared displacement were all non-significant predictors of density ($P > 0.10$, Table 1). When land cover class was included as a fixed effect, move time was not a predictor of density, most likely because land cover class accounted for differences in move time and move times were shortest (least time per step) in olive groves and longest in wheat fields.

Analysis of diffusion among species as a function of wingspan indicated that diffusion was strongly associated with wingspan and that larger butterflies had higher diffusion rates ($F = 21.23$, $P = 0.001$). Analysis of density among species as a function of wingspan indicated that wingspan is not strongly associated with density ($F = 0.028$, $P = 0.869$).

Discussion

Consistent with predictions from ecological theory, diffusion was negatively associated with density across 25 butterfly species in four land cover classes. This pattern is also consistent with the majority of studies we found that quantified relationships between diffusion and density in other taxa, for which seven of nine species showed the expected negative association (e.g., Zalucki & Kitching 1982; Turchin 1991; Hannunen & Ekbom 2001; Puche & Su 2001). Our results expand on these past studies by exploring multiple species over a broad geographic area with several land cover classes. The pattern we observe

of low density in areas with fast flight are comparable to conclusions by Cowley *et al.* (2001), who found that mobility in 49 British butterfly species was negatively associated with population density such that more mobile butterflies tended to be sparse across the landscape and thus low densities were associated with the highest movement rates. Of course, correlation is not causation, and the association between diffusion and density should be further explored to uncover biological mechanisms. Nonetheless, our results support the notion that movement contributes to among-land cover variation in density. Our study also demonstrates that across a diverse taxon, diffusion rates are not species-invariant traits, but rather are highly dependent on landscape context such that land cover classes in which diffusion rates are high typically have low densities.

Our study emphasizes that spatial variation in density is at least partly caused by variation in movement: all else being equal, if animals move more slowly in an area, they will be more abundant. Slow or short-distance movement is often associated with high density because slow movement makes animals spend more time in an area and results in aggregations (Kareiva & Odell 1987; Klaassen, Nolet & Bankert 2006; Abraham 2007; Kolzsch *et al.* 2015). Organisms' responses to habitat quality often drive movement patterns: when individuals find suitable resources, they slow down and paths are more tortuous (e.g., Kareiva & Odell 1987). This reduced diffusion is reflected in higher population densities. We did not quantify resources, but we documented the second step in this causal chain by associating slower movement with higher abundance. In many cases (e.g., Holmes, Marra & Sherry 1996; Rittenhouse *et al.* 2010; Konvicka *et al.* 2012; Unglaub *et al.* 2015), high population densities are assumed to reflect higher quality patches, and the causal relationships are similar to the diffusion-density relationship we observe: higher resource density leads to slower movement, which leads to higher densities of foraging organisms. In

other cases, high population density reflects lower per-capita habitat quality and higher movement rates; this pattern has been documented by manipulating habitat quality and density in experimental populations (Kuefler, Avgar & Fryxell 2012). Although it is possible to independently manipulate habitat quality and density and observe how animal behavior changes, it is less obvious how one could independently manipulate habitat quality and diffusion rates, to determine their independent contributions to variation in density. Nonetheless, experimentally decoupling habitat quality and movement behaviour to understand patterns of density would be useful because ecologists often want to infer habitat quality from habitat use (Boyce & McDonald 1999; Dias, Granadeiro & Palmeirim 2009) or predict movement based on habitat quality (e.g., Matter & Roland 2002; Klaassen, Nolet & Bankert 2006; Fahrig 2007).

The relationship between dispersal and density is a topic of intense interest and ecological importance given the pace of landscape change due to fragmentation and climate change (e.g., reviews by Denno & Peterson 1997 and Matthysen 2005). Based on a review of immigration rates in birds and mammals, Matthysen (2005) concluded that individuals dispersed more when population densities were high in 33 of 35 studies. Denno and Peterson (1995) drew similar conclusions from insect-based studies (72 species exhibit density-dependent dispersal). Matter and Roland (2002) experimentally manipulated resource abundance and sex ratio, and observed higher immigration to areas with higher resources. These studies do not test the relationship between habitat-specific diffusion *per se* and density but rather metrics of immigration or emigration related to local density. Emigration and immigration rates are the integration of habitat-specific diffusion rates and boundary behaviours (Kuefler *et al.* 2010). Our results indicate higher diffusion rates in land cover classes with low density, a process which can result in higher immigration rates (similar to

Matter & Roland 2002) because individuals move rapidly through low density regions and are often attracted to high density areas once encountered (c.f. Kuefler *et al.* 2010).

Simpler metrics of animal movement (e.g., move lengths and turning angles) were not reliable predictors for scaling from individual behaviour to population density in our study. Our result contrasts with previous studies; for example Konvicka *et al.* (2012) found a negative relationship between lifetime movement, another “simple” movement metric, and local patch densities for six butterfly species. However, a key difference is that we define move lengths over very small steps (on the scale of minutes) whereas Konvicka *et al.* use lifetime movement as a metric of mobility, which would effectively integrate move lengths (at short time scales), speeds, and path curvature. More generally, we were surprised that the simpler metrics were not significant predictors of density, because move lengths, turning angles, and diffusion tended to covary among high and low resource patches such that high quality patches had short move lengths and large turning angles while low quality patches had long move lengths and small turning angles (e.g., Hannunen & Ekbom 2001; Morales *et al.* 2004). Our results suggest that it may be important to combine all three aspects of diffusion (move length, move time, and turning angle) to predict patterns at higher levels of organization.

Dispersal distance generally increases with body size (Bowler & Benton 2005; Stevens *et al.* 2014) while population size declines with body size (Brown *et al.* 2004 but see Gaston & Lawton 1988; Blackburn & Gaston 2001). Our data support the prediction that larger animals should move further distances. This relationship has also been found in other Lepidopteran species (Kuussaari *et al.* 2014), though not consistently across all taxa (Teitelbaum *et al.* 2015). We did not, however, find support for a negative relationship

between body size and density. One explanation could be that the range of body sizes included in our study is much smaller than in other macroecological cross-taxon surveys (e.g., Brown *et al.* 2004). In addition, these studies often use dispersal kernels to predict range expansion in the context of climate change, and assume that dispersal is species-invariant rather than changing as a function of land cover type (Vinatier *et al.* 2011; Loos *et al.* 2015). In our study, the diffusion-density relationship is based mostly on variation within species, among land cover classes (e.g., *Melanargia titea* has a diffusion rate of 2.6 m²/sec in semi-natural habitat, 7.7 m²/sec in the field margin and 24.6 m²/sec in the wheat fields, Table S1), leading to differences in rates of diffusion rates both within and among species, and differences within species among land cover classes that were often greater than differences between species.

A large and growing number of studies have compiled movement tracks for vertebrate animals (Hussey *et al.* 2015; Kays *et al.* 2015). As published, it is difficult to extract habitat-specific diffusion rates for species in these datasets, presumably because diffusion is viewed as too simplistic and/or too abstract to be suitable for interpreting these data. However, in several isolated case studies, diffusion models work well for both invertebrates (e.g., this study, Turchin 1991) and vertebrates (e.g., Bergman, Schaefer & Luttich 2000; Austin, Bowen & McMillan 2004; Frair *et al.* 2005; Klaassen, Nolet & Bankert 2006; Forester *et al.* 2007; Halstead *et al.* 2007, Avgar *et al.* 2013). Such data could be valuable for conservation. For instance, a common assumption of connectivity and corridor studies is that the suitability of conduit land cover classes for promoting movement is directly related to their suitability as habitat (Driscoll *et al.* 2014; Bernal-Escobar, Payan & Cordovez 2015). A diffusion perspective suggests a different outlook; given that an individual is willing to enter a corridor, the most effective corridor may be one that promotes movement, e.g., an area with high

diffusion rates and therefore a high likelihood that the individual will reach suitable target patches to colonize or reproduce. While diffusion may be a simple tool, it is a useful across multiple taxa as a first approximation of movement, and we encourage others to apply it more widely to understand and interpret patterns of animal movement and abundance across landscapes.

Data Accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1m081> (Schultz *et al.* 2016).

Author contributions

GP conceived of field design, secured funding for field studies and collected all field data; CS initiated collaboration with GP; EC and CS conceived of ideas and design for analyzing data and writing the manuscript aided by GP; CD prepared data for use in diffusion models; LB, EC & CS analyzed the data; CS led manuscript writing. All contributed to drafts and to final manuscript preparation.

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Tables

Table 1. Models testing relationship of diffusion or component parameters (move length, turning angle or move time) with density. Wingspan is a fixed effect in models and models are fit using best model for structure of random effects (Table S2). Shown are χ^2 from type II χ^2 tests from analysis of deviance.

	Model	χ^2	df	P(χ^2)
Diffusion	Diffusion	6.84	1	0.0089
	Wingspan	2.74	1	0.0976
	Diffusion \times Wingspan	3.05	1	0.0809
Move Length	Move Length	1.29	1	0.2556
	Wingspan	0.03	1	0.8716
	Length \times Wingspan	0.47	1	0.4913
Turning Angle	Cos (Turn Angle)	3.63	1	0.0566
	Wingspan	0.30	1	0.5812
	Cos (Turn Angle) \times Wingspan	1.21	1	0.2726
Move Time	Move Time	5.76	1	0.0164
	Wingspan	0.27	1	0.6011
	Move Time \times Wingspan	0.02	1	0.8966
E(R²)	E(R ²)	1.57	1	0.2201
	Wingspan	0.17	1	0.6803
	E(R ²) \times Wingspan	2.15	1	0.1430

Table 2. Models testing relationship of diffusion or component parameters (length, turning angle or time) with density. Wingspan and land cover class are fixed effects and models are fit using best model for structure of random effects Models are fit using same factors for random effects as in Table S2. Models were fit using backwards procedure with non-significant interaction terms ($P > 0.10$) sequentially removed and final model presented below. Shown are χ^2 from type II χ^2 tests from analysis of deviance.

	Model	χ^2	df	$P(\chi^2)$
Diffusion	Land cover class	84.75	3	< 0.0001
	Diffusion	6.57	1	0.0104
	Wingspan	9.20	1	0.0024
	Diffusion \times Land cover class	4.39	3	0.0361
	Diffusion \times Wingspan	8.41	1	0.0383
Move Length	Land cover class	69.57	3	<0.0001
	Move Length	0.91	1	0.3398
	Wingspan	4.56	1	0.0328
Turning Angle	Land cover class	70.17	3	<0.0001
	Cos (Turn Angle)	1.56	1	0.2108
	Wingspan	2.93	1	0.0871
Move Time	Land cover class	87.29	3	<0.0001
	Move Time	3.35	1	0.0672
	Wingspan	3.97	1	0.0464
E(R²)	Land cover class	65.87	3	<0.0001
	E(R ²)	<0.01	1	0.9251
	Wingspan	2.50	1	0.1135

Figures Legends

Figure 1: Location of field sites in Israel (a) and examples of the sampled land cover classes: (b) wheat fields, (c) olive groves, (d) semi-natural area, and (e) field margin (here, at the edge of a wheat field). Color in (a) represents the rainfall gradient (see Pe'er et al. 2011).

Figure 2: a) The sampling transect protocol (example) and example of flight paths b) in wheat and c) in olive sites. Each series of linked points representing one movement path of an individual. Note the clear difference in path structure in semi-nature vs. within the wheat field. Yellow line is edge of agricultural area, green line is edge of semi-natural area; area in between these is the field margin.

Figure 3. Sample sizes of 25 species included in analyses. Included are those species \times land cover class combinations with at least four complete moves (4 turning angles, 5 move lengths and 5 move times).

Figure 4. Relationship between diffusion and butterfly density. Each point represents one species \times land cover class combination for which there were at least four moves. Black curve based on model fit to whole dataset. Gray curves are output of predicted model fit to species-specific wingspans and model coefficients.

Figure 1.

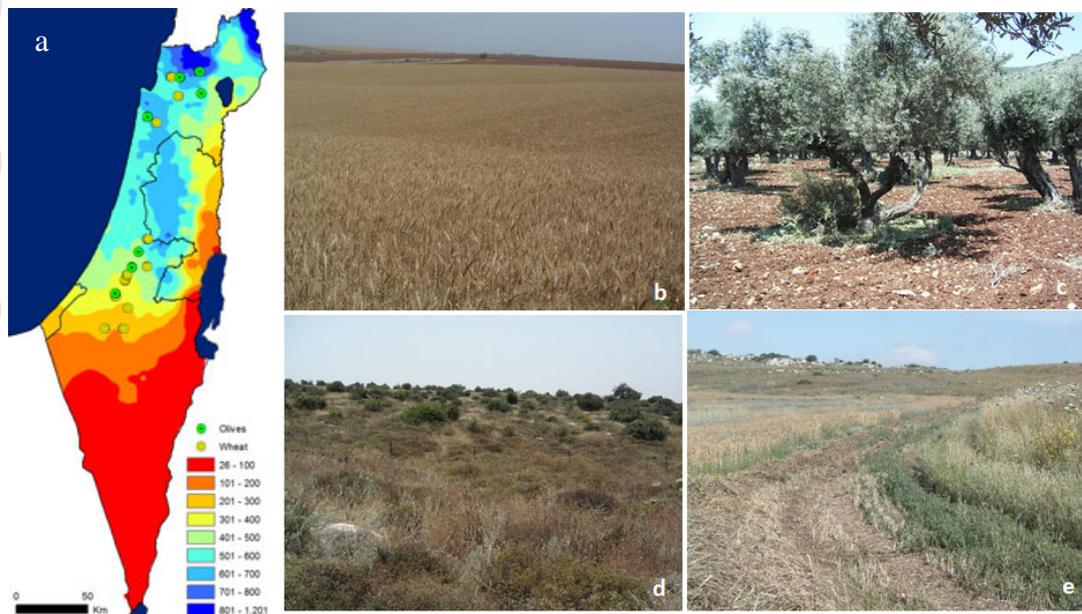


Figure 2.

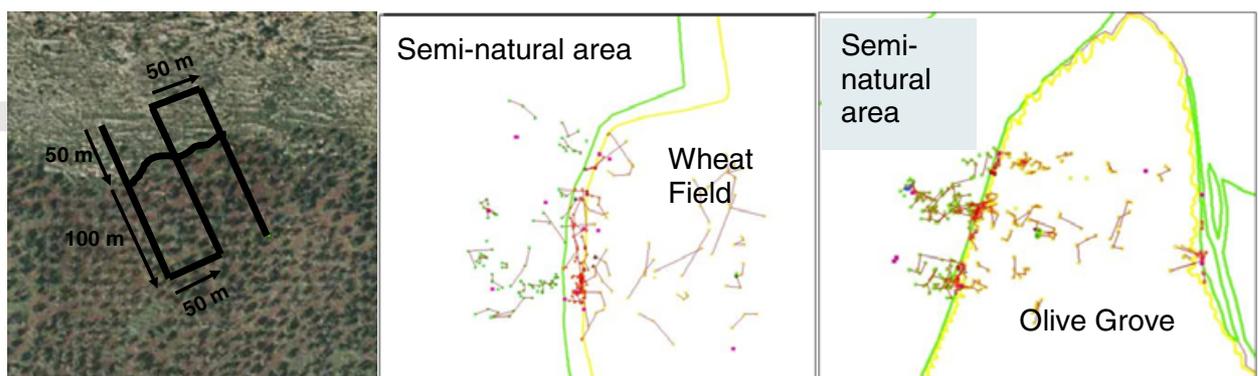


Figure 3.

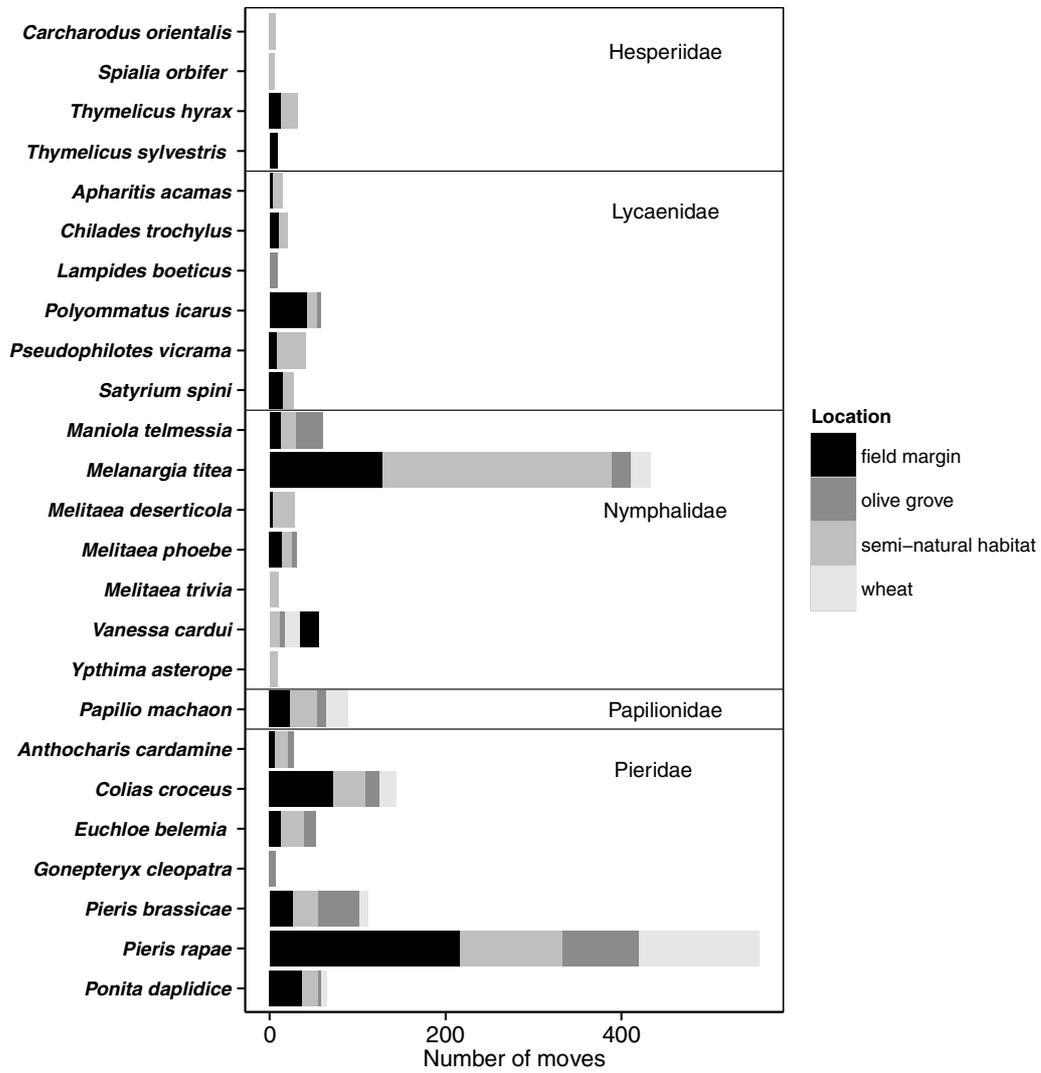


Figure 4.

