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RESEARCH ARTICLE

The proximate causes of asymmetric movement across heterogeneous landscapes

Miguel A. Acevedo · Robert J. Fletcher Jr.

Abstract

Context Asymmetric movements, in which the probability of moving from patch i to patch j is not necessarily the same as moving in the opposite direction, may be the rule more than the exception in nature where organisms move through spatially heterogeneous environments. Empirical tests of dispersal asymmetries are rare with even fewer tests of the mechanisms driving such patterns.

Objectives We tested for the mechanisms of asymmetric movement in the cactus-feeding insect, *Chelinidea vittiger*, using a combination of observational and experimental approaches.

Methods In the observational approach, we analyzed movements from mark-recapture data in a large plot for over 4–5 generations and tested for the role of differences in patch area and wind direction driving broad-scale asymmetric movements. In the field experiment, we translocated individuals to experimental arenas where we tested for the roles of patch area, wind, presence of conspecifics, and matrix height driving directed movements at fine spatio-temporal scales.

Results We found that population-level patterns of movements in *C. vittiger* were generally asymmetric. At broad scales, observational data suggested that these asymmetries were related to variations in patch size, with movements being directed from small to large patches. At fine scales, experiments showed that movement was also directed from small to large patches, but this effect was mediated by the structure of the surrounding matrix.

Conclusions Our results illustrate how and why movement asymmetries can occur across landscapes. Accounting for such asymmetries may improve our understanding and prediction of spatially structured population dynamics and landscape connectivity.

Keywords Asymmetric · *Chelinidea vittiger* · Dispersal · Connectivity · Matrix · *Opuntia* · Patch area · Wind direction

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Introduction

Variations in movement have broad implications for many areas of ecology and evolution, including altering local adaptation via gene flow (Kawecki and Holt 2002; Henry et al. 2015), community structure (Tilman et al. 1994; Liebhold et al. 2004; Salomon

et al. [2010]), and population dynamics (Wiegand et al. [1999]; Revilla et al. [2004]; Armsworth and Roughgarden [2005]; Wang et al. [2015]). In metapopulation theory, movement is critical because it provides the means for (meta)population persistence over time (Hanski [1998]).

In spatially structured populations, asymmetric movement can occur, in which the probability of moving, p, from patch i to patch j is not necessarily the same as moving in the opposite direction (i.e., $p_{ij} \neq p_{ji}$). A symmetric pattern of movement may be expected when all the factors that affect dispersal are identical in all directions (Gustafson and Gardner [1996]; Bode et al. [2008]); however, such symmetry might be rarely observed in nature. Recent theoretical models suggest that movement asymmetries can have substantial effects on metapopulation dynamics (Armsworth and Roughgarden [2005]; Vuilleumier and Possingham [2006]; Vuilleumier et al. [2010]), increasing stability (Dey et al. [2014]; Wang et al. [2015]) and promoting genetic diversity (Wilkinson-Herbots and Ettridge [2004]). Empirically, it has been shown that assuming symmetry when movement is asymmetric may result in biased colonization and extinction estimates (Acevedo et al. [2015]) and can lower the predictive accuracy of connectivity assessments (Fletcher et al. [2011]).

A variety of mechanisms may give rise to asymmetrical pattern of movement. In passive dispersers, asymmetric movement may be the result of the directed effect of an advection source such as wind or water currents (Keddy [1981]; Armsworth and Bode [1999]; Schick and Lindley [2007]; Treml et al. [2008]). In active dispersers, asymmetric movement may be the result of environmental heterogeneity, such as variation in habitat quality or patch size (Pulliam [1988]; Gustafson and Gardner [1996]; Holt [1996]; Ferreras [2001]; Prevedello and Vieira [2010]; Kadoya and Washitani [2012]). Individuals may have adapted to seek better habitats by actively dispersing from low to high-quality patches (often larger in size; e.g., Gustafson and Gardner [1996]; Ferreras [2001]). Movement asymmetries may also be the result of changes in the organisms' movement behavior due to environmental cues (e.g., taxis; Compton [2002]). For instance, many species of insects are attracted to visual or chemical cues that direct their movement (Prokopy and Owens [1983]). Some Homoptera, Hymenoptera and Hemiptera direct their movement upwind while tracking volatile chemical signals from vegetation

(anemotaxis; e.g., Compton [2002]; Williams et al. [2007]; Moser et al. [2009]). The likelihood of an individual to move to a particular patch may also depend on the patch occupancy state or the abundance of conspecifics (Smith and Peacock [1990]; Serrano et al. [2001]; Serrano and Tella [2003]).

Here we test for mechanisms of asymmetric movement in the cactus-feeding insect, *Chelinidea vittiger*, using a combination of observational and experimental approaches. Recently, Fletcher et al. ([2011]) found that movement in this species was highly directional across a patch network, which altered assessments of landscape connectivity (see also Schooley and Wiens [2003]). However, the mechanisms for this directionality in movement were not considered. We hypothesized that three primary mechanisms may cause directed movements: (1) positive anemotaxis (movement upwind; Schooley and Wiens [2004]), (2) movement toward larger patches (Schooley and Wiens [2005]), and (3) conspecific attraction (Stamps [1988]). Wind may help *C. vittiger* detect volatile olfactory cues from *Opuntia* cactus patches where it lives, potentially resulting in individuals directing their movements towards patches that are located upwind (Schooley and Wiens [2004]). Similarly, *C. vittiger* may actively search for larger patches of *Opuntia*, because of enhanced resource availability (see Schooley and Wiens [2005]). Because of the aggregative behaviors of this species (Fletcher and Miller [2008]; Miller et al. [2012]), conspecific attraction may occur and also cause directed movements. To address these mechanisms, we first re-analyzed data from a mark-recapture study across a 56-patch network (Fletcher et al. [2011]) to test for the magnitude of movement asymmetry and its potential relationship with wind direction and/or patch area at a relatively broad scale. Second, at a finer spatio-temporal scale, we conducted a translocation experiment in which we manipulated patch area, wind advection, and the presence of conspecifics to determine if, and the extent to which, *C. vittiger* biases movements in response to these factors.

Methods

Study area and focal species

The study was conducted in the Ordway-Swisher Biological Station, OSBS (29.4°N, 82.0°W), located

in Melrose County, Florida, USA. At this station, *C. vittiger* uses *Opuntia humifusa* cactus patches, primarily occurring in old-field habitats. *O. humifusa* is native to the eastern USA and typically grows in dry, sandy soils in sandhills, old fields, prairies or scrub. *C. vittiger* depends on this cactus species for its whole life cycle, including feeding and breeding (with two to three generations per year).

We focused our research on movements by adult *C. vittiger*. Adults of *C. vittiger* are winged but rarely fly; instead, adults typically walk between cactus patches through an unsuitable matrix (De Vol and Goeden 1973; Schooley and Wiens 2004). Previous studies show that this matrix structure, typically measured as herbaceous vegetation height, negatively influences adult movements and population dynamics (Schooley and Wiens 2004; Fletcher et al. 2014). Median movement distances range from 1 to 2.5 m/day (Schooley and Wiens 2004, 2005), which makes movement tractable and an ideal system to study short-term dispersal (Fig. 1).

Broad-scale study: patterns of movement asymmetries

To describe broad-scale patterns of movement asymmetries, we re-analyzed data considered by Fletcher et al. (2011, 2013b) in the context of connectivity modeling. The data consisted of individual movements of marked *C. vittiger* in all patches ($n = 56$) within a 30×30 m plot (Fig. 1). Patches were defined following Schooley and Wiens (2004), where cladodes (i.e., cactus pads) were considered the same patch if they were <25 cm apart. Surveys were conducted from September 2008 until November 2009 every 2–3 weeks (except during the winter) for a total of 21 surveys. During each survey, all individuals on each patch were counted (both nymphs and adults), and all adults were sexed and individually marked on the pronotum with nontoxic permanent marker. Even though this plot was not a closed system, additional recapture rates in the surrounding area were low.

To test for potential mechanisms driving broad-scale asymmetric movements, we estimated patch (i.e., cactus pad) area using the equation for an ellipse (area = major radius × minor radius × π; Schooley and Wiens 2005). The major and minor radii were measured using a ruler. We used data from the nearest
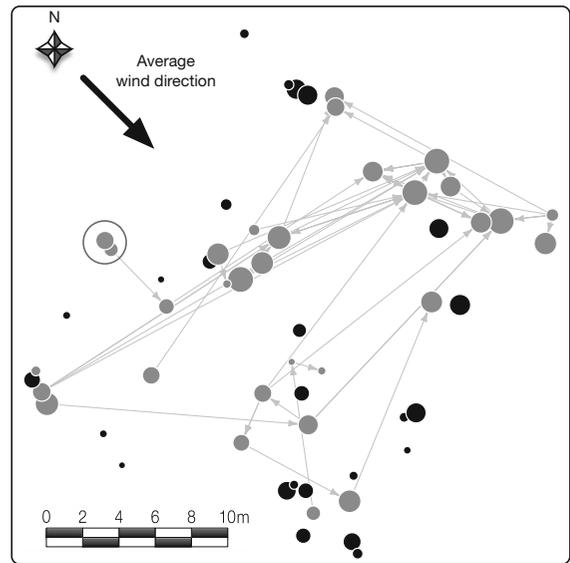

Fig. 1 Observed inter-patch transitions of *C. vittiger* in a 30×30 m plot. *Gray circles* represent patches that included movement whereas *black circles* are patches that did not. The *black arrow* represents the average direction of the prevailing winds. The *circle* encloses the only pair of patches that showed symmetric movements ($W_{ij} = W_{ji}$). Note how the remaining connections go in only one direction, showing a pattern of high asymmetric movement

weather station to the site (1 km) to estimate average wind direction. We averaged daily wind direction from January 1, 2009 to November 27, 2009 (there was no data available for 2008) to produce an estimate of wind direction relative to each pair-wise combination of patches in the network. Analyzing the contribution of conspecifics was unfeasible with this broad-scale data set, because out of the 70 movements observed, only 20 were to a previously occupied patch. This was a small sample size to analyze, because 18 of these showed a single inter-patch movement, which does not allow enough variability to interpret potential effects of conspecifics. We did include conspecifics as a treatment in the fine-scale field experiment (see below).

We represented the movements of *C. vittiger* as a matrix **W** where w_{ij} represents the total number of movements from patch i to patch j. We calculated the proportion of symmetric links as the number of links in **W** in which $w_{ij} = w_{ji}$ for all $j \neq i$ that were different from zero (i.e., the number of movements was the same in both directions) divided by the total number of links that had movement. While Fletcher et al. (2011) noted that movement appeared highly directional, they

did not assess if this putative pattern was greater than what would be expected by chance nor did they test for mechanisms of this pattern. To test if this proportion was different from the proportion of symmetric links expected by chance, we used a randomization test, which is commonly applied for inferring patterns on networks (e.g., Croft et al. 2011). To do so, we compared the proportion of symmetric links in this matrix of movements **W** to the proportion of symmetric links in 1000 randomly generated movement matrices. These random matrices had the same number of movements as **W**, but the positions of the links were randomly assigned among the links that had movement (i.e., shuffling the weights of the matrix while keeping the same topology; e.g., Fletcher et al. 2013b). We used a z-score test to compare the proportion of observed symmetric links in **W** with the distribution of symmetric links in the randomly generated movement matrices. This test asks whether the observed proportion of symmetric links is significantly different from the expected by chance and how many standard deviations away the observed value is from the mean of the random distribution.

We calculated the difference in movement between patches i and j as $\Delta w_{ij} = w_{ij} - w_{ji}$. Similarly, we calculated the difference in patch area as $\Delta A_{ij} = A_i - A_j$, where A_i is the area of patch i. We also calculated the difference (δ_{ij}) between the average angle of wind direction and the angle between patches i and j in radians with respect to the horizontal axis. For simplicity, δ_{ij} is scaled by π to constrain $\delta_{ij} \in [0, 1]$ (Acevedo et al. 2015). If $\delta_{ij} = 0$, patches i and j are exactly aligned downwind with the average angle of prevailing winds. As δ_{ij} increases, patches are arranged increasingly upwind. We modeled the difference in movement Δw_{ij} as a function of differences in patch area and wind direction using a generalized linear model with a Skellam distributed response. The Skellam distribution is appropriate to model the difference between movements because it describes the difference between two Poisson processes (Skellam 1945).

We fitted six types of models that represented hypotheses for mechanisms influencing the potential for asymmetric movements at broad scales as a function of (1) patch area (ΔA_{ij}), (2) patch area squared to account for non-linearity in the response to patch area differences (ΔA_{ij}^2), (3) wind direction (δ_{ij}), (4) the additive effect of patch area and wind direction

($\Delta A_{ij} + \delta_{ij}$), (5) the interactive effect of patch area and wind direction ($\Delta A_{ij} \times \delta_{ij}$), and (6) a single intercept representing the null hypothesis that that area or wind are not driving the broad-scale movements of *C. vittiger*. These models were fitted by maximum likelihood using the VGAM package in R (R Development Core Team, 2014, Yee 2015). We used Akaike's information criterion corrected for small sample sizes (AICc) to compare model fit and choose the most parsimonious model.

Field experiment: environmental features driving fine-scale movement asymmetries

We used a randomized block design in which each block contained four plots, one for each treatment (wind, patch area, and conspecifics) and a control (Fig. 2). Each plot included four patches of *Opuntia humifusa* cladodes located in the four cardinal directions. The release patch was located in the center of the plot and consisted of a single cladode (Fig. 2). We used a small release patch to catalyze movement (see Castellon and Sieving 2006) because a single cladode is below the minimum patch area requirements for *C. vittiger* (Schooley and Wiens 2005). All experimental patches were located 1 m away from the release patch, which is within the perceptual range of this species (Fletcher et al. 2013a).

All plots consisted of 32 cladodes that were distributed among four patches, arranged in different proportions among the patches depending on the treatment. In the wind and conspecific treatments, and in the control plot, each experimental patch was composed of eight cladodes per patch (Fig. 2a, b, c). In the area treatment, one patch consisted of 16 cladodes (large patch), another consisted of eight cladodes (medium patch) and two patches consisted of four cladodes (small patches; Fig. 2d). All of these cladodes were considered high-quality habitat for the species because they were fresh, with no visible feeding marks and were collected in nearby old fields (<100 m).

The wind treatment consisted of placing a battery operated fan (Caframo Kona black color, 7 cm diameter) located 5–10 cm away from a randomly selected experimental patch and 10 cm from the soil with wind directed towards the release patch (Fig. 2b). The fan was operated by a 12 V battery and continuously ran during the sampling period (48 h). Wind

Fig. 2 Diagram showing the study design composed of four plots, one for each treatment: (**a**) control, (**b**) wind, (**c**) conspecifics, and (**d**) variations in patch area. The wind treatment included a fan blowing at a similar speed than the average speed of prevailing winds. The conspecifics treatment included a male and a female in different patches assigned randomly. Note how all plots include the same amount of habitat (32 cladodes). In the patch area treatment these were rearranged. The study included 3 blocks of this design and all treatments were assigned randomly
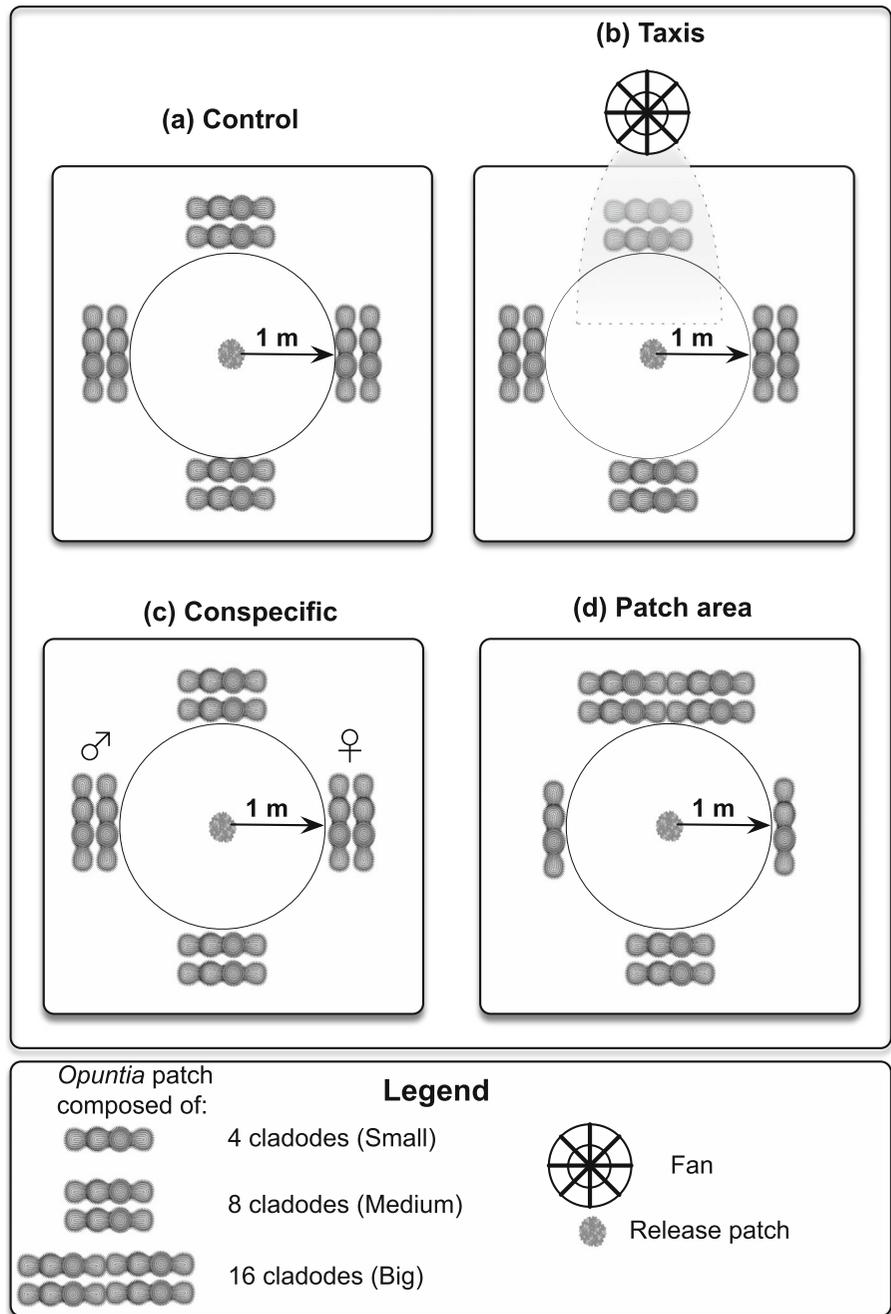
speed at the wind treatment experimental patch was 14.8 km/h and 4.7 km/h at the release patch. These wind speeds are within the range previously reported in the literature in a study that found a strong relationship between wind direction and *C. vittiger* movement (0.5–7.75 km/h; Schooley and Wiens 2005).

The conspecifics treatment consisted of placing one individual male in one patch and one individual female in another patch in the same plot (Fig. 2c). We included males and females separately because previous studies have found differences in aggregative behavior for males and females (Miller et al. 2012). Treatments were assigned to the patches randomly.

The individual cladodes that contained the conspecifics were enclosed with fine mesh to prevent the individual from leaving the patch (Miller et al. 2012). The mesh allowed for visual and/or pheromone cues to be potentially detected by the released individuals.

We considered control patches that were not subject to the treatment within each plot. For example, in the wind treatment plots, only one out of the four treatments had a fan, and the other three patches in the plot were considered control plots. Similarly, in the conspecific treatments the two patches that did not have conspecifics were considered control patches. In the area treatment, patches with eight cladodes were considered controls. In addition to the control patches, we included in the block design a control plot in which all patches were composed of 8 cladodes and releases and censuses were done in the same way as in the treatment plots.

We also performed two types of procedural controls, one for the conspecifics and another for the wind treatment, to ensure the observed rates of immigration for each treatment were driven by the treatments and not an artifact of incorporating a fan or mesh covering on cacti in the plot. We conducted the procedural control experiment for the wind treatment in the same plot plots (i.e., same location and same cactus patches in each block) where the wind experiment took place. The only difference was that the fan was placed blowing in the direction away from the release patch. By doing this, we keep the potential effects of having a non-natural object in the landscape (i.e., black fan producing noise), but removed the effect of wind. Similarly, we conducted the procedural control experiment for the conspecifics treatment in the same plots where the conspecific treatment experiments took place (i.e., different plots than the wind procedural control experiments). We enclosed the same two patches at used for the conspecific treatments with mesh, with the only difference that a conspecific individual was not included. Sampling was done in the same was as in the other experimental treatments (see above).

At the beginning of the study, plots were depleted of any other cactus and individuals of *C. vittiger* within 10 m of the release patch. Plots were located at least 35 m apart from the nearest experimental plot. Locations of the treatments at both the plot and patch level were assigned at random.

Individuals were captured in nearby cactus patches (<100 m). These were bred and reared in containers in a screen house (see Fletcher and Miller 2008). Nymphs were raised in groups with fresh and healthy *O. humifasa* cladodes. As soon as they became adults, they were marked on their pronotum using non-toxic permanent marker and transferred to individual containers until they were released in the experimental plots. A greenhouse experiment found that marking individuals in this way does not alter survival rates ($P > 0.5$; Fletcher, unpublished).

In each trial, two males and two females were released at the center, release patch. The location of each of these individuals in the plot was surveyed after 24 h and then after 48 h of being released. Each observed individual was removed from the plot as soon as its location was noted. We conducted 7 (5 for experimental treatments and 2 for the procedural control) trials in each of the three blocks between July and November 2012.

Previous studies have found that matrix resistance may be an important determinant in the movement of *C. vittiger* (Schooley and Wiens 2005; Fletcher et al. 2014). To account for this potential effect, we measured matrix height at 15 points within a 100 × 50 cm strip transect (5 measures in each edge of the transect and 5 in the center spaced every 20 cm) between the release patch and the experimental patch. For each point, we quantified the number of times vegetation touched a graded pole in each 10 cm category (vertically) to a maximum of 90 cm. We averaged the number of layers and the maximum height of each set of 15 measures to characterize the matrix between the release patch and each experimental patch. Both measures (number of layers and maximum height) were highly correlated ($r_p = 0.85$); therefore, here we present only the data for maximum height to be consistent with other investigations on this species (Schooley and Wiens 2005; Fletcher et al. 2014).

To test for the effect of the treatments (variations in patch area, wind and conspecific presence) on the directed movements of *C. vittiger*, we modeled the rate of movement from the release to each of the experimental patches. This rate of movement described the proportion of the released individuals that moved from the release patch to an experimental patch in a period of 48 h. This is an appropriate response given that experimental patches were located 1 m away from the target patch and the average individual movement rate is <1 m/day (Schooley and Wiens 2004; Fig. 2b).

Each treatment was analyzed independently because variation within plots for different treatments made pooling data across treatments impractical. In the conspecific treatment, we fitted three types of models to describe the rate of movement of males only, females only, and for both sexes together, because previous research has shown different aggregative behaviors between males and females of *C. vittiger* (Miller et al. 2012). For each treatment consideration (area, wind, and conspecifics male, females and both), we fitted five types of models that represented different hypotheses explaining the rate of movement. An (1) intercept-only model represented the null hypothesis that the experimental treatments are not influencing the movements of *C. vittiger*. We also fitted a model representing the (2) treatment. Because each treatment was modeled independently, the variable used was different for each treatment. In the area treatment, variation in patch area was represented by the number of cladodes in each patch (4, 8 or 16 cladodes). In the wind treatment, the presence of wind was represented by a binary variable indicating the presence or not of the fan in the experimental patch. In the conspecific treatment (response of males, females and both), the presence of a conspecific was treated as categorical variable with three factors: male, female and control. The effect of the matrix, represented by the maximum average vegetation height between the release patch and the experimental patch, was incorporated into models both as a (3) single main effect, and also as an (4) additive and (5) interacting covariate with the treatment.

We used a negative binomial regression to model the rate of movement toward experimental patches with an offset representing the total number of individuals released (4 individuals, except for the response of males and female conspecifics in which two individuals were released). The negative binomial distribution was an appropriate choice because the count data showed over-dispersion. In a preliminary analysis, we incorporated the date of the survey, block and plot as random effects, but the variance explained by these random effects was $<10^{-8}$ and thus their incorporation did not improved model fit. Models were fitted by maximum likelihood using the MASS package in R. We used Akaike's Information Criterion corrected for small sample sizes (AICc) to compare

model fit and choose the most parsimonious model describing movements rates per treatment.

Results

Broad-scale patterns

The 30 × 30 m patch network was composed of 56 patches with area ranging from 1.25 to 252 cm². Average wind direction was 131 ± 99° SD, with average prevailing wind speeds of 4.07 ± 3.03 SD km/h. We observed a total of 70 movements in this patch network from September 2008–November 2009 (see Fletcher et al. 2011 for more details). The proportion of symmetric connections in this network (0.04) was lower than the average in randomly generated movement networks (0.10 ± 0.04 SD; $z = -1.77$, $P = 0.04$).

The most parsimonious model explaining the difference in inter-patch movements included area squared as a covariate (Table 1; Table S1). This model predicts symmetric movements when there is no difference in patch sizes. The model also predicts an increase in the strength of asymmetric movements from small to large patches as the different between patches increases (Fig. 3). A model that included patch area as a single covariate predicted a similar pattern and had similar fits (ΔAIC < 2; Table 1).

Table 1 Model results testing for the relationships between the magnitude of movement asymmetry (ΔW_{ij}) as a function of the difference in patch area (ΔA_{ij}), and the difference between the angle among patches and the average angle of prevailing winds (δ_{ij})

Covariates	k	ΔAICc	ΔAICc weight
ΔA_{ij}^2	3	0	0.44
ΔA_{ij}	2	1.08	0.25
$\Delta A_{ij} + \delta_{ij}$	3	3.02	0.10
Null (intercept only)	1	3.05	0.10
δ_{ij}	2	3.86	0.06
$\Delta A_{ij} \times \delta_{ij}$	4	4.17	0.05

Note that $\Delta A_{ij} + \delta_{ij}$ describes an additive effect, while $\Delta A_{ij} \times \delta_{ij}$ describes an interacting effect. All models are generalized linear models following a Skellam distribution

Field experiment

A total of 240 individuals were marked and released in the field experiment of which 86 were recaptured. Of these, we recaptured 19 individuals in the area treatment, 16 individuals in the wind treatment, 25 (14 females and 11 males) in the conspecifics treatment, and 26 in the control plot. The most parsimonious model explaining the rate of movement in the area treatment included the number of cladodes (patch size) interacting with the maximum height of the vegetation in the matrix as covariates (Table 2). This model predicted a relatively small and constant rate of movement to all size patches when the vegetation height in the matrix was low, but a higher rate of movement towards bigger patches when the matrix vegetation was higher than the median (Fig. 4). A null model (intercept only) was the most parsimonious model explaining the rate of movement in the wind treatment and control plots. Similarly, a null model was also the most parsimonious explaining the rate of movement in the conspecific treatments when modeling the response of both males and females together and when modeling the movement of females. When modeling the rate of movement of males in the conspecifics treatment, the most parsimonious model
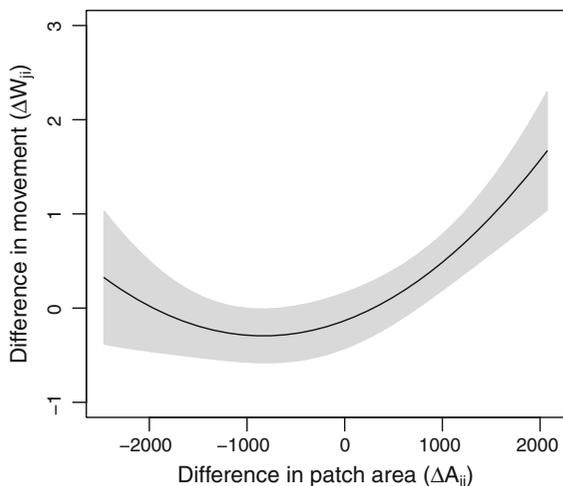
incorporated the presence of conspecifics (Table S2); however, this model had no better fit than the null (intercept-only) model (ΔAIC < 2; Table 2; Table S3). The null (intercept-only) model was the most parsimonious model explaining the rate of movement in both procedural controls (Table 2).

Discussion

Asymmetric dispersal may be the rule rather than the exception in nature. While recent theoretical models suggest that movement asymmetries can have substantial effects on patch connectivity and metapopulation dynamics, empirical tests of dispersal asymmetries across landscapes remain rare, with even fewer tests of the mechanisms driving such patterns. We found that movement patterns of *C. vittiger* at the population-level were generally asymmetric. Both broad-scale observations across a patch network and a small-scale experiment showed that movement was directed from small to large patches, emphasizing that variation in patch size is a primary factor driving asymmetric movement in this system.

Both the observational and experimental results showed no support for prevailing or artificial wind driving movement decisions. Even though previous studies have shown that *C. vittiger* directs its movements towards prevailing winds (Schooley and Wiens 2003) in open short-grass prairies in Colorado, Fletcher et al. (2013b) also found little support for this wind hypothesis while studying the perceptual range of *C. vittiger* in our study area. They suggested that wind speeds at old-field habitats in our study area are relatively lower than in the open short-grass prairie habitat where Schooley and Wiens (2003) conducted their study. Nevertheless, in our experiments, artificial wind speeds at 10 cm from the ground were within the range of those in the open short-grass prairie (Schooley and Wiens 2003). This discrepancy may be explained by at least two alternative hypotheses related to habitat differences between open short-grass prairie in Colorado and old-field habitats in Florida. First, *C. vittiger* populations at OSBS may have developed alternative ways to detect patches that do not include relying on wind because wind-speed variation is less in this system. Alternatively, the type or amount of olfactory cues may differ between *O. humifusa* and *O. polycantha* (the *Opuntia* species in

Fig. 3 The best-fit model explaining the different in movements (ΔW_{ji}), between patches j and i, as a function of patch area squared (ΔA_{ji}^2). Note how dispersal asymmetries increase with increasing difference in patch area with an exponential increase in movements from small to large patches. *Solid line* represents predicted means and shading describes 95% confidence intervals

Table 2 Model results explaining the rate of immigration to patches in each treatment

Treatment	Sex response	Covariates	k	ΔAICc	ΔAICc weight
Area	Both	Area × matrix	4	0	0.60
		Area + matrix	3	1.4	0.29
		Area	2	3.5	0.10
		Matrix	2	12	0.001
		Null (intercept only)	1	12.1	0.001
Wind	Both	Null (intercept only)	1	0	0.46
		Wind	2	1.2	0.25
		Matrix	2	1.9	0.18
		Wind + matrix	3	3.4	0.08
		Wind × matrix	4	5.6	0.03
Conspecifics	Both	Null (intercept only)	1	0	0.54
		Matrix	2	1.4	0.27
		Conspecifics	3	2.7	0.14
		Conspecifics + matrix	4	4.6	0.05
		Conspecifics × matrix	6	9.2	0.001
	Males	Conspecifics	3	0	0.50
		Null (intercept only)	1	1.7	0.210
		Conspecifics + matrix	4	2.2	0.169
		Matrix	2	3.8	0.073
		Conspecifics × matrix	6	4.7	0.048
	Females	Null (intercept only)	1	0	0.490
		Conspecifics	3	1.6	0.222
		Matrix	2	2	0.177
		Conspecifics + matrix	4	3.6	0.081
		Conspecifics × matrix	6	5.6	0.030
Control	Both	Null (intercept only)	1	0	0.74
		Matrix	2	2.1	0.26
Procedural control	Both	Null (intercept only)	1	0	0.58
		Fan	2	0.68	0.42
		Null (intercept only)	1	0	0.68
		Mesh	2	1.5	0.32

Matrix refers to vegetation height between patches, and area the number of cladodes. k describes the number of parameters and ΔAICc wt the AICc relative weight. Note that, for example, Area + Matrix describes an additive effect, while Area × Matrix describes an interacting effect

Schooley and Wiens 2003). In addition, wind direction was highly variable, which may prevent its use as a reliable directional cue (See Supplementary material, Appendix 2, Fig. S1). Even though we found no effect of wind influencing movement for this species, it may still be an important driver in other taxa, particularly wind-dispersed plants (e.g., Acevedo et al. 2015). More generally, other advection sources such as marine or river currents may be important drivers of asymmetric movements in other taxa.

We found no strong support for the presence of adult conspecifics driving the directed movements of *C. vittiger*. Nevertheless, multiple studies have found

that this species uses social information to guide its behavior (e.g., Fletcher and Miller 2008; Miller et al. 2012), suggesting that there may be other conspecific interactions driving directed movements not tested here (e.g., effe–cts of conspecific densities, male and female presence, etc.). Given that conspecific interactions have been documented for both aggregative and non-aggregative species (e.g., Serrano and Tella 2003; Fletcher 2009), and can affect colonization rates (Hahn and Silverman 2006), functional connectivity estimates (Zeigler et al. 2011) and metapopulation dynamics (Ray et al. 1991; Alonso et al. 2004), its potential implications as a driver of asymmetric
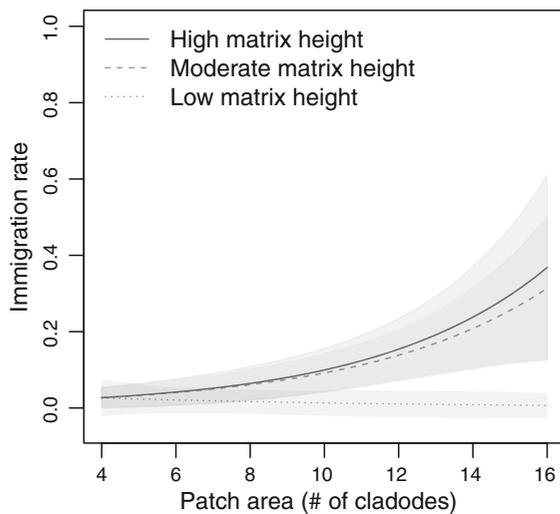
Fig. 4 Partial relationships of the best-fit model explaining the rate of movement in the area treatments of the field experiment. This model included patch area (number of cladodes) interacting with vegetation height. *Lines* represent 1st quartile (low matrix height), median (moderate matrix height) and 3 quartile (high matrix height) of maximum vegetation height. *Lines* represents predicted means and shading describes 95% confidence intervals

dispersal remains an alternative hypothesis to be further tested.

Patch size can be an important determinant of patch immigration rates (Bowman et al. 2002; Bowler and Benton 2005). Both observational and experimental results showed support for the hypothesis that variation in patch area is a driving mechanism of directed movements that result in an asymmetric pattern of movement. These asymmetries were the result of higher movement rates from small to large patches. Two potential mechanisms may account for this pattern. First, organisms may be dispersing by a passive-diffusive process (Kindvall and Petersson 2000; Travis and French 2000), which makes large patches (i.e., patches with greater circumference) more prone to be detected by a randomly moving individual. On the other hand, there is ample evidence showing that animals tend to move actively toward larger patches (e.g., Diffendorfer et al. 1995; Baguette et al. 2000), suggesting that other factors may be covarying with patch size and/or individuals may have strong preference for larger patches (Bowler and Benton 2005). If individuals of *C. vittiger* were randomly finding patches in the area treatment, we would have expected the immigration rate to be

proportional to the linear dimension of the patch, because all patches were located at the same distance from the release patch (Bowman et al. 2002). Given that in our experimental design the linear dimension of the patches was proportional to the number of cladodes, we would have expected the average movement rate towards the 16-cladode patches to be $4\times$ that of the 4-cladode patches. Instead, we found that the rate of movement towards the 16-cladodes patch was $11\times$ that of the 4-cladodes patches (Fig. 5c). Moreover, the average movement rate towards the 16-cladode patches was $2.5\times$ that of the 8-cladode patches, suggesting a non-linear relationship between patch size and immigration rate (Fig. 5c). *C. vittiger* may direct their movements towards large cactus patches simply because larger patches provide a greater amount of food resources. Alternatively, large patches may provide more oviposition resources (e.g., spines; Fletcher and Miller 2008) for females to lay eggs or may include complex vertical structures that may serve as refugia from predators, thereby decreasing predation risk.

Our results support the idea that a combination of matrix characteristics and other landscape features such as patch size and isolation are important drivers of inter-patch movements (Bender and Fahrig 2005), potentially driving asymmetric patterns of dispersal (Gustafson and Gardner 1996). Patch immigration rates increased with increasing patch size and increasing vegetation height in the matrix (Fig. 4). Previous work in Colorado found that increasing vegetation height increases resistance to movement in this species (Schooley and Wiens 2004), while other studies in this system reveal more complex effects, where matrix structure interacted with patch configuration of cacti to alter movement rates (Fletcher et al. 2014). Our results strengthen the argument for a more prominent consideration of matrix effects in metapopulation studies.

The cost of dispersal is an important determinant of whether dispersal leads to fitness benefits (Bowler and Benton 2005). Our study system could be an example in which, even though increased matrix structure may provide resistance to movement (Schooley and Wiens 2005), it may increase survival by decreasing predation risk. Predation estimates for *C. vittiger* are scarce, but spiders have been shown to depredate them and other cactus-feeding insects (De Vol and Goeden 1973; Miller 2008). Regardless of treatment, most plots in which we observed no recaptures had little or
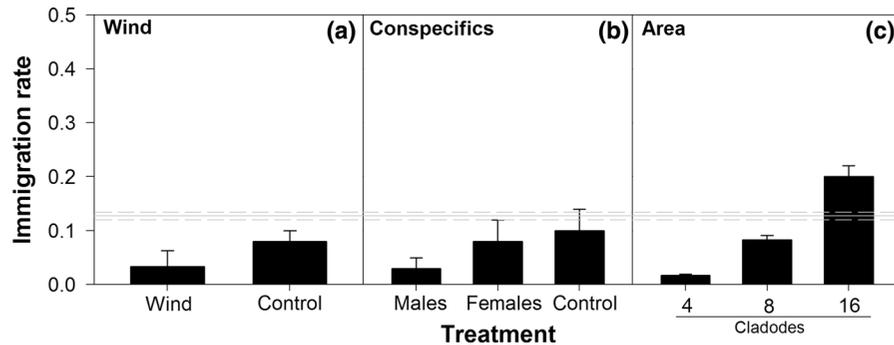
Fig. 5 Average rate of movement (±SE) at the patch level in the experimental treatments. The *solid gray line* represents the mean immigration rate for patches in the control treatment and the *dashed line* the associated standard errors

no matrix structure (i.e., they were open, with no herbaceous vegetation surrounding cacti). These individuals either were depredated or permanently emigrated from the experimental plot, suggesting that the risk of longer-distance dispersal may be less than the risk of being exposed moving through the matrix without cover. On the contrary, moving through a more complex matrix may provide cover in which individuals could move more safely and assess their surroundings for a patch to settle. A similar pattern has been found in other taxa. For instance, predation risk for forest birds is higher while trying to cross an agricultural matrix than secondary forests with relatively more vertical structure (Rodríguez et al. 2001).

Here we used an experimental model system (Wiens et al. 1993), where the spatial extent of the observational study and the experimental arenas might seem relatively small compared to extent needed for a similar study in other taxa. However, prior research on this species has repeatedly shown that moved is localized (e.g., Fletcher et al. 2011: median movement distance ∼ .5 m/2–3 weeks; Schooley and Wiens 2004: mean movement distance 1–2.5 m/day). In addition, in this area, experiments show that *C. vittiger* has a small perceptual range (∼1–2 m; Fletcher et al. 2013a). The observed 70 movements in the broad-scale study were the result of observations over 4–5 generations. It would take multiple years to conduct a similar study in an organism with one or less generations per year like birds (Fletcher et al. 2011). While patterns of *C. vittiger* movement have been shown to be similar to those observed in some vertebrates (e.g., Fletcher et al. 2011, 2013b), tests of asymmetric movements in organisms moving across broader scales would be useful.

Inter-patch matrix heterogeneity and movement behavior has strong implications for population dynamics and biodiversity patterns (Armsworth and Roughgarden 2005; Salomon et al. 2010). We found that patch size and matrix structure were the most important predictors of inter-patch movements and immigration rate in *C. vittiger*, leading to directed movements that resulted in an asymmetric pattern of dispersal. Variation in landscape features such as matrix structure and patch size are common in nature and may be important drivers of asymmetric dispersal in other systems, resulting in broad implications for landscape connectivity and (meta)population dynamics.

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