

Diffusion models for animals in complex landscapes: incorporating heterogeneity among substrates, individuals and edge behaviours

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Summary

1. Animals move commonly through a variety of landscape elements and edges in search of food, mates and other resources. We developed a diffusion model for the movement of an insect herbivore, the planthopper *Prokelisia crocea*, that inhabits a landscape composed of patches of its host plant, prairie cordgrass *Spartina pectinata*, embedded in a matrix of mudflat or smooth brome *Bromus inermis*.
2. We used mark–release–resight experiments to quantify planthopper movements within cordgrass–brome and cordgrass–mudflat arenas. A diffusion model was then fitted that included varying diffusion rates for cordgrass and matrix, edge behaviour in the form of a biased random walk and heterogeneity among planthoppers (sessile vs. mobile). The model parameters were estimated by maximum likelihood using the numerical solution of the diffusion model as a probability density. Akaike's information criterion (AIC) values were used to compare models with different subsets of features.
3. There was clear support for models incorporating edge behaviour and both sessile and mobile insects. The most striking difference between the cordgrass–brome and cordgrass–mudflat experiments involved edge behaviour. Planthoppers crossed the cordgrass–brome edge readily in either direction, but traversed the cordgrass–mudflat edge primarily in one direction (mudflat to cordgrass). Diffusion rates were also significantly higher on mudflat than for cordgrass and brome.
4. The differences in behaviour for cordgrass–brome vs. cordgrass–mudflat edges have implications for the connectivity of cordgrass patches as well as their persistence. Higher dispersal rates are expected between cordgrass patches separated by brome relative to mudflat, but patches surrounded by mudflat appear more likely to persist through time.
5. The experimental design and diffusion models used here could potentially be extended to any organism where mass mark–recapture experiments are feasible, as well as complex natural landscapes.

Key-words: dispersal, landscape, edge behaviour, *Prokelisia*, *Spartina*

Introduction

Animals must move commonly through a variety of landscape elements and cross boundaries between them in search of food, mates, reproductive sites and refuge from natural enemies. A growing body of literature suggests that the dispersal behaviour of organisms depends critically upon the composition of the landscape elements (Roland, Keyghobadi

& Fownes 2000; Ricketts 2001; Haynes & Cronin 2003) and the nature of the boundaries between elements, including the degree of contrast (Lawrence & Bach 1989; Ries & Debinski 2001; Haynes & Cronin 2006). Recent modelling attempts have begun to incorporate these landscape features as well as more realistic dispersal behaviour (Tischendorf 1997; Cantrell & Cosner 1999; With & King 1999; Ovaskainen & Cornell 2003; Ovaskainen 2004). One common method is to model movement as a diffusion process, an approach that has provided accurate descriptions of dispersal for a broad range of organisms (Kareiva 1982; Turchin 1998; Bergman,

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Schaefer & Luttich 2000; Skalski & Gilliam 2000). A recent feature of these models is the inclusion of explicit boundary or edge behaviour in the diffusion framework (Cantrell & Cosner 1999; Ovaskainen & Cornell 2003; Ovaskainen 2004). In most cases the modelled landscape is still relatively simple, however, consisting of a single patch embedded in a homogeneous and unsuitable matrix (but see Ovaskainen 2004).

Here, we develop and parameterize a detailed, spatially explicit model of movement for a herbivore in a complex landscape, the planthopper *Prokelisia crocea* Van Duzee (Hemiptera: Delphacidae). This insect inhabits a system comprised of patches of its sole host plant, prairie cordgrass (*Spartina pectinata*), embedded in a matrix of mudflat, other native grasses and the exotic grass smooth brome (*Bromus inermis*). Matrix composition is known to influence greatly planthopper emigration and interpatch movement rates in this system. Planthoppers rarely emigrate across a cordgrass–mudflat boundary, but exhibit no such restraint in emigrating across a cordgrass–brome one (Haynes & Cronin 2003, 2006). In addition, emigrants colonize host patches embedded in brome more readily than mudflat, due probably to their more circuitous movement paths within brome. Local and regional population dynamics of the planthopper are also strongly matrix-dependent. Patches in brome typically have lower and more variable densities and populations that are very extinction prone, relative to patches in mudflat (Cronin & Haynes 2004). Populations in mudflat-embedded patches appear to function as sources in this system, while brome-embedded patches are sieves (i.e. patches leak individuals faster than can be countered by reproduction and emigration) (Cronin 2007).

We feel that a detailed spatially explicit model of planthopper movement is needed, for two reasons. First, the landscape inhabited by this insect is composed of cordgrass patches that differ greatly in size, distance from other patches and the surrounding matrix. These features are needed in the model if we are to compare its predictions with planthopper movements in the real system, including a number of previous studies (Baum *et al.* 2004; Cronin & Haynes 2004). Secondly, it would form a component of a population dynamics model for this system, where it is clear that local dynamics are influenced strongly by dispersal and the matrix environment (Cronin 2004, 2007; Cronin & Haynes 2004; Haynes *et al.* 2007). The dispersal models we develop are based on diffusion equations and make use of improved software for solving these equations (COMSOL AB 2007) as well as recent advances in modelling edge behaviour (Ovaskainen & Cornell 2003; Ovaskainen 2004). We take a Eulerian approach to the problem, describing the behaviour of the population rather than individual insects, because this type of data is obtained more easily in most systems. For example, it can be difficult to record the individual paths of small insects, but mass mark–recapture experiments (Turchin 1998) can provide information on the density of insects at various points in space and time after release. Although we will parameterize the models using data from the planthopper system, this approach could, potentially, be extended to any organism where such mark–recapture experiments are feasible.

Materials and methods

STUDY SYSTEM

Prairie cordgrass is a common native species in wet prairie fragments of the North American Great Plains (Mobberly 1956; Hitchcock 1963) and in North Dakota occurs in clearly defined patches, ranging in size from 0·1 m² to 4 ha. These patches are embedded within three main types of matrix habitat: (1) mudflats sometimes inhabited by saltwort (*Salicornia rubra* Nels.); (2) mixtures of predominantly native grass species (primarily foxtail barley *Hordeum jubatum* L., western wheatgrass *Agropyron smithii* Rydb. and little bluestem *Schizachyrium scoparium* Michx.); and (3) stands of exotic smooth brome (*B. inermis* Leyss.). Brome was established intentionally in prairie fragments throughout the Great Plains to provide animal graze and to prevent soil erosion in disturbed areas (D'Antonio & Vitousek 1992; Larson, Anderson & Newton 2001; Haynes & Cronin 2003). Within our study areas, brome has exhibited rapid spread into fragments over a 6-year period (2000–06), displacing cordgrass and other native grasses (F. Dillemuth & J. T. Cronin, unpublished manuscript).

The phloem-feeding planthopper *P. crocea* feeds and reproduces only on prairie cordgrass, and is the dominant herbivore on this plant (Holder & Wilson 1992; Cronin 2003a,b,c). The planthopper is bivoltine in North Dakota, with peaks in adult abundance in mid-June and early August. Adults are wing-dimorphic, but populations are composed primarily of macropterous individuals (> 90%). In a field mark–release–recapture experiment, Cronin (2003a) found that adult females spread diffusively within cordgrass patches with a daily median displacement of < 1 m.

PLANTHOPPER DISPERSAL AND EDGE BEHAVIOUR EXPERIMENTS

We quantified planthopper movement behaviour in response to the patch edge using a mark–release–resight experiment. The experiment was also intended to provide information on dispersal rates in cordgrass and two common matrix types, brome and mudflat. The basic design involved simultaneous releases of marked insects within cordgrass, at the cordgrass–matrix edge and within the matrix. The positions of the marked insects were then recorded and the resulting data used to parameterize a diffusion model (see below).

In July 2006, we selected large cordgrass patches (≥ 100 m²) from the Kelly's Slough National Wildlife Refuge that had linear edges adjacent to areas of either mudflat or brome. We then placed a 200 × 100 cm coordinate grid across the cordgrass–matrix edge, with the grid extending 100 cm into cordgrass and the same distance into the matrix. The grid was constructed of monofilament fishing line anchored to a polyvinylchloride (PVC) frame at 10-cm intervals. It was positioned 0·5 m above the ground and had no discernible effect on the redistribution of planthoppers.

On the morning of the experiment, planthoppers were collected with a sweep net from nearby cordgrass habitat. Only adult females were included in the experiment because they represent the primary source of population spread for this species (Cronin 2003a; Haynes & Cronin 2003). Females were marked with fluorescent powder (Day-glo Color Corporation, Cleveland, OH, USA), a marking technique that results in no adverse effects on planthopper dispersal ability or survival (Cronin 2003a). One hundred marked planthoppers were released simultaneously at each of three locations with respect to the cordgrass edge: 25 cm in cordgrass, on cordgrass plants at the

patch edge and 25 cm in the matrix. A different powder colour was used to mark planthoppers at each location. The insects were released near the midline of the arena. The experimental releases generated moderate densities of planthoppers that are encountered commonly in natural populations.

Planthoppers were chilled on ice prior to their release. As the insects warmed up, they would crawl up onto nearby vegetation (except in the case of the releases in the mudflat). Planthoppers never exhibited an escape response following their release (see also Cronin 2003a). The position of the marked planthoppers was recorded at approximately 45-min intervals. Because movements are known to be faster in the mudflat (Haynes & Cronin 2006), we made our first observations in the mudflat arenas at 5 min and then at 45 min thereafter. Positions were determined to the nearest 10 cm using the coordinate grid. Observations of released planthoppers were terminated after 4 h. Replicates (the three releases associated with the same grid) were conducted in pairs each day, one for each type of arena (cordgrass–brome vs. cordgrass–mudflat). Five replicate releases were performed for each arena type.

QUANTIFYING DISPERSAL BEHAVIOUR USING DIFFUSION MODELS

We used a diffusion model to quantify planthopper movements using the data from the dispersal experiments. The first step was to define the landscape through which the organisms are dispersing, which amounted to selecting the diffusion framework within COMSOL 3·4 (COMSOL AB 2007), drawing a 200×100 -cm rectangle corresponding to the experimental arena, and then a larger 240×140 -cm rectangle surrounding the arena. We then specified that the four edges of the larger rectangle were absorbing boundaries, which seemed appropriate because insects this far from the arena were unlikely to return. A line was then drawn through the rectangles to represent the cordgrass–matrix boundary. We modelled the behaviour on this boundary as a biased random walk (Ovaskainen & Cornell 2003; Ovaskainen 2004), where a parameter k_1 describes the probability of an insect on the cordgrass–matrix boundary moving towards cordgrass, while $k_2 = 1 - k_1$ is the probability of entering the matrix (brome or mudflat). Values of k_1 near 1 imply that movement is biased strongly towards cordgrass, while $k_1 = 0.5$ implies no bias in movement and thus no edge behaviour. The actual boundary conditions are:

$$u_1 - (k_1/k_2)u_2 \rightarrow 0, \quad \text{eqn 1}$$

where u_1 and u_2 are the densities on each side of the boundary. Note that boundary behaviour depends only on the ratio k_1/k_2 . In terms of this parameter combination, there is no bias in movement if $k_1/k_2 = 1$, while movement is biased toward cordgrass as k_1/k_2 becomes large. The flux of individuals across the boundary is also assumed to be continuous. This boundary condition implies a discontinuity in densities as one traverses the boundary, and Ovaskainen (2004) developed a finite element method that incorporates this behaviour. However, it was possible to implement this boundary condition in COMSOL 3·4 by controlling the flux on the boundary (personal communication, COMSOL AB). In particular, we defined the inward flux on the cordgrass side of the boundary as $-K(u_1 - (k_1/k_2)u_2)$, while the inward flux on the matrix side was similar but opposite in sign. The parameter K determines how strongly equation 2 is enforced, and so we chose a large value for this parameter ($K = 10^6$).

The initial distribution of insects was approximated as a bivariate normal distribution ($\sigma = 1$ cm) centred on the release point for all

three locations within the arena (within cordgrass, at the cordgrass–matrix edge and within the matrix). Given this initial condition and the boundary conditions described above, one could find the probability density of planthoppers at any location and time by numerically solving the two-dimensional diffusion equation:

$$\frac{\partial u_i}{\partial t} = D_i \left(\frac{\partial^2 u_i}{\partial x^2} + \frac{\partial^2 u_i}{\partial y^2} \right) \quad \text{eqn 2}$$

for each side of the arena ($i = 1$ for cordgrass, $i = 2$ for matrix), where u_i is the density of planthoppers and D_i is the diffusion rate. However, preliminary examination of the data (as well as observations during the experiment) suggested that a substantial fraction of insects remained stationary throughout the experiment within cordgrass and brome (but not mudflat). We therefore developed models where the population was divided into two classes, with a proportion p sessile and $1 - p$ mobile. The sessile insects were distributed according to the initial distribution for the entire experiment, while the mobile insects dispersed away from the release point according to equation 2. The overall solution was obtained by adding the solutions for the mobile and sessile insects. Insects released in mudflat were treated as entirely mobile.

We used maximum likelihood (Bickel & Doksum 1977) to estimate the model parameters from our observations of planthopper position, treating the above solution as a probability density for the distribution of insects within the arena. Observations for different planthoppers and times were treated as independent in the likelihood function L . This assumption should be approximately correct given that only a fraction (about 20%) of the released insects were observed at any one time, making it unlikely that a particular insect was observed more than one to two times. We combined the data from the three release locations (cordgrass, edge, matrix) in calculating the likelihood, so that the parameters were estimated using all the available data from each replicate. One complication was that planthoppers were observed only inside the arena, excluding any insects that left during the experiment. To match this feature of the observations we used the conditional distribution of planthoppers within the arena, obtained by dividing the diffusion solution by its integral over the arena for each time interval (Kareiva 1982). Another difficulty was the number of parameters in the model, potentially requiring a four-dimensional search for the values that maximize the likelihood. Preliminary analyses as well as previous studies (Haynes & Cronin 2006) suggested that the movement rates for cordgrass and brome were similar, and so we assumed a common diffusion rate for the two substrates for cordgrass–brome arenas. We did not assume this for cordgrass–mudflat arenas, as the rates of movement appeared quite different for this combination.

The maximum likelihood estimates were found numerically using the simplex algorithm (Nelder & Mead 1965) implemented in MATLAB 7·5 (The Mathworks, Inc. 2007). The algorithm minimized $-\log L$ as a function of the model parameters. At each step in the minimization process, a MATLAB driver program used COMSOL 3·4 to find the numerical solution, then calculated the likelihood at that point in parameter space. A grid search was used to initialize the search algorithm to ensure that the minimization converged on a global minimum, although the likelihood surface appeared to have an uncomplicated shape. In four of the five cordgrass–mudflat replicates, we found that $-\log L$ decreased monotonically as the ratio k_1/k_2 increased, probably because few or no insects crossed from cordgrass into mudflat in these replicates (suggesting $k_1 \rightarrow 1$ and so $k_1/k_2 \rightarrow \infty$). We therefore set $k_1/k_2 = 50$ in these replicates and proceeded to estimate the other parameters in the model. We note that the accuracy of the COMSOL 3·4 solution can be increased by

reducing the tolerance values within the software, at the cost of time. We determined empirically the accuracy needed for the likelihood process by decreasing these tolerance values until the parameter estimates and minimum $-\log L$ -value appeared stable. We also used a smaller finite element mesh than the default setting to ensure that the probability density was always positive.

STATISTICAL METHODS

For each of the replicates, we also fitted reduced models with either no edge behaviour ($k_1/k_2 = 1$), or edge behaviour but no sessile insects ($p = 0$). We then constructed Akaike's information criterion (AIC) values using the values of $-\log L$ -values for the full model and the two reduced models, as well as the number of parameters in each model (Akaike 1974; Burnham & Anderson 1998). We then compared the fit of the full model (which always had the lowest AIC value) with the two reduced models by calculating ΔAIC values. In addition, we fitted a reduced model for the cordgrass–brome replicates that had both mobile and sessile insects in cordgrass, but only mobile insects for brome. The intention here was to examine the evidence for sessile insects on brome.

We compared the parameter estimates between cordgrass–mudflat and cordgrass–brome replicates using a randomized block model with cordgrass–matrix type as the fixed effect, while the day (block) on which each replicate was carried out was a random effect. The analysis was conducted using PROC MIXED in SAS 9.1 (SAS Institute, Inc. 2005). The variance component due to blocks was very small, however, and so these analyses essentially reduced to one-way analysis of variance (ANOVA) with matrix type as the treatment; 95% confidence intervals for the parameter estimates were also calculated for each arena type. A log transformation was applied to the diffusion rates and k_1/k_2 values, while an arcsine square root transformation was used for p .

We generated plots of the observed and expected number of planthoppers in the following way. We first divided the experimental arenas into concentric squares surrounding each release point, with the squares composed of the individual squares defined by the sampling grid (see above). The first square was the release square of the sampling grid, the second square the eight grid squares surrounding the release square and so on, for up to six squares (labelled 1, 2, 3, etc.). If a square was bisected by the cordgrass–matrix boundary each portion was dealt with separately, with the portion on the far side of the boundary labelled as 4', 5' and so forth. We then used the fitted diffusion model to calculate the expected number of planthoppers in each concentric square by integrating the probability density for each square, and compared this with the observed number in the same squares (see Figs 1 and 2). We also calculated the correlation between the observed and expected frequencies and squared this to obtain the coefficient of determination (R^2), as a simple measure of model fit. For each release point (cordgrass, edge and matrix), we calculated a separate R^2 using all the observation times within each replicate. Another approach that we attempted was to compare the observed and expected distributions for each time and release point using goodness-of-fit tests. We were unable to conduct these tests because the frequencies were usually too low at any one time.

Results

We observed 19.5 ± 6.7 [standard deviation (SD)] planthoppers at each observation time, on average across all release locations and replicates ($n = 10$). The fewest were observed for

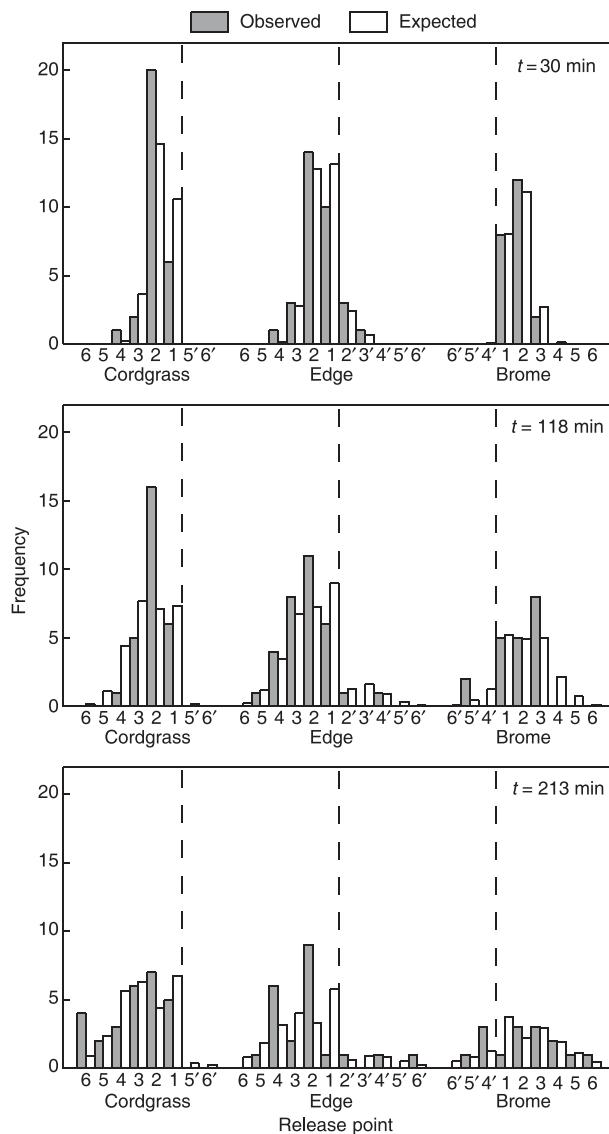


Fig. 1. Observed and expected frequencies of planthoppers in concentric squares (1, 2, 3, ...) surrounding the release points for a cordgrass–brome arena (replicate 4). Squares labelled as 2', 3', etc. are the portions of the squares on the far side of the cordgrass–matrix boundary. The edge is denoted by a dashed vertical line. Distributions are reported for three time-periods that correspond to the beginning ($t = 30$ min), midpoint ($t = 118$ min) and near the end ($t = 213$ min) of the 4-h observation period. See Materials and methods for further details.

mudflat releases (11.9 ± 6.6 , $n = 5$), probably because insects released on this matrix type moved rapidly and often left the arena. The parameter estimates for the full diffusion model (including edge behaviour and mobile vs. sessile insects) are shown in Table 1. No significant difference was found in the diffusion coefficients for cordgrass between arena types (cordgrass–brome vs. cordgrass–mudflat) ($D_{\text{cordgrass}}: F_{1,8} = 2.25$, $P = 0.1720$). There was a significant difference between the diffusion rate estimated for brome vs. mudflat ($D_{\text{matrix}}: F_{1,8} = 6.26$, $P = 0.0368$), with diffusion rates on mudflat typically larger, although they were also highly variable across replicates

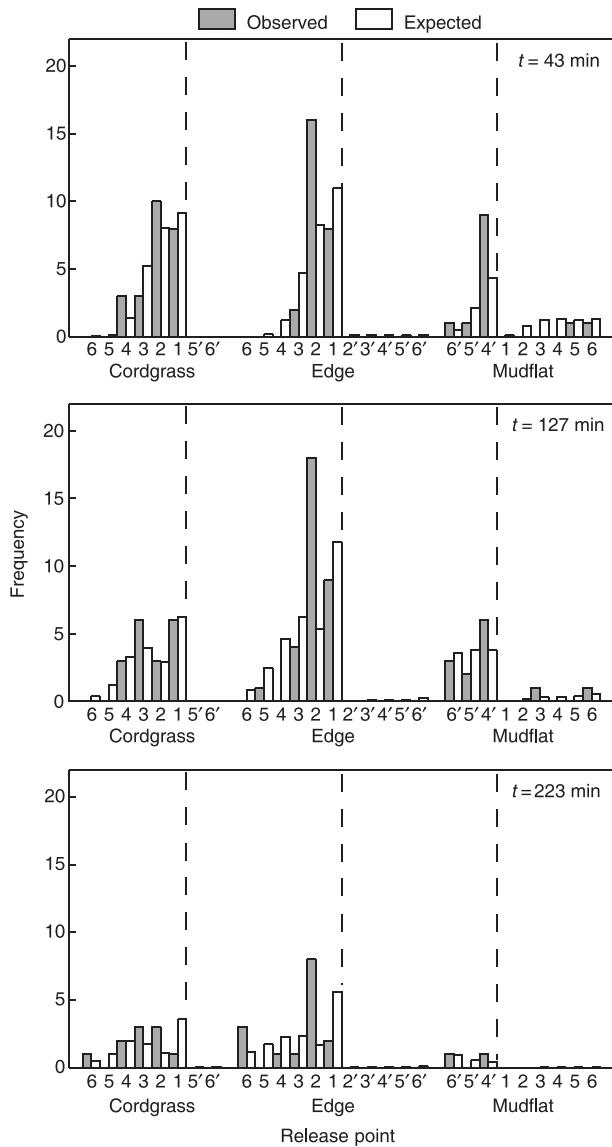


Fig. 2. Observed and expected frequencies of planthoppers in concentric squares ($1, 2, 3, \dots$) surrounding the release points for a cordgrass–mudflat arena (replicate 5). Squares labelled as $2', 3', \dots$ are the portions of the squares on the far side of the cordgrass–matrix boundary from the release point. The edge is denoted by a dashed vertical line. Distributions are reported for three time-periods that correspond to the beginning ($t = 43$ min), midpoint ($t = 127$ min) and near the end ($t = 223$ min) of the 4-h observation period. See Materials and methods for further details.

(Table 1). There was also a significant difference between the proportion of sessile planthoppers ($p: F_{1,8} = 6.00, P = 0.0400$), with higher values observed for cordgrass–mudflat arenas (Table 1). The estimated values suggest that a sizeable fraction (14–43%) of the insects were sessile during the experiment. There was clear support for models with a sessile class vs. models without one, given the large difference in AIC values between the two (Table 1, $\Delta\text{AIC}_1, \Delta\text{AIC}_2$).

We found a highly significant difference in the ratio k_1/k_2 between the two arena types ($F_{1,8} = 43.71, P = 0.0002$), with

the ratio much higher for cordgrass–mudflat arenas (Table 1). This was expected, given that few insects were observed to cross from cordgrass to mudflat in these experiments (but crossed readily from mudflat to cordgrass), while many insects crossed from cordgrass to brome and vice versa. There was strong support for edge behaviour in both cordgrass–matrix types, however, because the change in AIC values comparing models with and without edge behaviour were quite large (ΔAIC_3). Moreover, the 95% confidence intervals for the five replicates combined did not include 1 ($k_1/k_2 = 1$ implies no edge behaviour) for either cordgrass–matrix type (Table 1). Equivalently, the 95% confidence intervals for k_1 did not include 0.5 (no edge behaviour), implying that individuals on the cordgrass–matrix edge were more likely to enter cordgrass than the matrix, for both matrix types.

Figures 1 and 2 show the observed and expected distribution of insects at three different times for one replicate each of the cordgrass–brome and cordgrass–mudflat arenas, selected because the parameter estimates for these replicates were typical. The fitted model appears to describe the data adequately in most cases, although there were times when the observed and expected distributions appeared different (e.g. the edge release in Fig. 2 at $t = 127$ min). We suspect that these discrepancies arose because of small-scale heterogeneity in the distribution of the plants, or even the orientation of the plant stems (angled or upright), especially at the release points. When we examined the plots for the other eight replicates (not shown) there was no systematic pattern (such as particular times or release locations) to the discrepancies. The average R^2 value was approximately 0.62, indicating substantial agreement between the fitted model and the observed frequencies (Table 1). The two worst fits occurred for one release in brome and one in mudflat. Figure 2 illustrates the strong edge behaviour seen in cordgrass–mudflat arenas. Note the asymmetry in the observed frequency distribution, with no insects crossing from cordgrass to mudflat in the edge release, while they crossed readily from mudflat to cordgrass in the mudflat release. In addition, the insects moved more rapidly in mudflat vs. cordgrass, mainly disappearing from mudflat by the end of experiment.

Discussion

The most striking difference found between the cordgrass–brome and cordgrass–mudflat experiments was in edge behaviour. In the cordgrass–mudflat replicates few or no planthoppers crossed the edge from cordgrass to mudflat, and as a result the edge behaviour parameter k_1 was close to one (k_1/k_2 large), suggesting a strong bias in movement at cordgrass–mudflat boundaries. This was not the case for brome, although our results suggest that there is some edge behaviour because $k_1 > 0.5$ ($k_1/k_2 > 1$) for all five replicates. The results for cordgrass–mudflat arenas indicate more extreme edge behaviour than was found by Ovaskainen (2004) for the butterfly *Melitaea diamina* ($k_1 \approx 0.9$) for habitat vs. matrix, and equal to or greater than found in several more qualitative studies of edge behaviour (Bach 1988; Haddad

Table 1. Parameter estimates and confidence intervals (CI) for releases of marked planthoppers in arenas of cordgrass adjoining a matrix of brome or mudflat for the full diffusion model, including varying diffusion rates, edge behaviour and both sessile and mobile insects. Here n is the total number of observations for insects released at all locations, p is the estimated proportion of sessile insects, $D_{\text{cordgrass}}$ the diffusion rate of mobile insects on cordgrass (cm^2/min), D_{matrix} the corresponding rate for matrix and k_1/k_2 the parameter controlling edge behaviour, while k_1 is the probability of returning to cordgrass for an insect on the cordgrass–matrix edge. Also shown are changes in Akaike's information criterion (AIC) values between the full model and one without any sessile insects (ΔAIC_1), without sessile insects on brome (ΔAIC_2) and without edge behaviour (ΔAIC_3). The last three columns are R^2 values calculated using the observed frequencies of planthoppers and the expected ones predicted by the full model, for concentric squares surrounding each release point (cordgrass, edge and matrix)

Matrix	Rep	n	p	$D_{\text{cordgrass}}$ (cm^2/min)	D_{matrix} (cm^2/min)	k_1/k_2	k_1	ΔAIC_1	ΔAIC_2	ΔAIC_3	R^2_{cord}	R^2_{edge}	R^2_{matrix}
Brome	1	427	0.168	1.226	1.226*	2.932	0.746	403.6	82.2	23.4	0.63	0.57	0.71
	2	304	0.144	2.839	2.839*	3.144	0.759	287.2	82.8	27.6	0.41	0.58	0.65
	3	269	0.274	1.282	1.282*	9.298	0.903	441.2	66.6	45.0	0.69	0.54	0.20
	4	376	0.220	1.275	1.275*	3.594	0.782	437.8	173.8	22.2	0.69	0.67	0.88
	5	465	0.367	0.837	0.837*	9.140	0.901	926.8	345.2	45.6	0.76	0.79	0.85
Mean			0.230	1.366	1.366	4.897	0.830						
95% CI			Lower	0.131	0.785	0.785	2.377	0.704					
			Upper	0.347	2.377	2.377	10.089	0.910					
Mudflat	1	467	0.350	1.948	2.640	50.0†	0.980	658.0	—	162.2	0.34	0.82	0.76
	2	252	0.358	1.140	3.092	50.0†	0.980	523.8	—	99.6	0.67	0.58	0.03
	3	190	0.432	3.392	19.054	19.286	0.951	465.0	—	43.0	0.73	0.53	0.65
	4	355	0.286	2.651	1.640	50.0†	0.980	286.0	—	64.0	0.59	0.62	0.78
	5	353	0.317	1.829	16.795	50.0†	0.980	444.6	—	199.6	0.88	0.52	0.62
Mean			0.348	2.053	5.326	41.326	0.976						
95% CI			Lower	0.282	1.231	1.307	24.349	0.961					
			Upper	0.417	3.426	21.698	70.140	0.986					

*The diffusion model assumes equal diffusion rates for cordgrass and brome (see Materials and Methods). †Fixed at 50.0 during the estimation process (see Materials and methods).

1999; Roland *et al.* 2000; Ries & Debinski 2001; Berggren *et al.* 2002; Goodwin & Fahrig 2002). We also found that the proportion of sessile insects was higher for cordgrass–mudflat arenas, possibly indicating another difference in behaviour for this type of edge. The mechanism underlying this change in behaviour is unknown.

The differences in dispersal behaviour for cordgrass–brome vs. cordgrass–mudflat edges have implications for the connectivity of cordgrass patches as well as their persistence. We would expect to see higher dispersal and colonization rates between cordgrass patches separated by brome than mudflat, because fewer insects would leave patches surrounded by mudflat, and this does appear to be the case (Cronin & Haynes 2004; Baum *et al.* 2004). We would also expect that small cordgrass patches surrounded by brome would ‘leak’ planthoppers and be more likely to go extinct, while those surrounded by mudflat would retain them and persist over time. Indeed, this is the pattern seen in field studies that have examined the persistence of the planthopper for networks of cordgrass patches or isolated patches surrounded by brome vs. mudflat (Cronin & Haynes 2004; Cronin 2004, 2007; Haynes *et al.* 2007). From a conservation viewpoint, our results suggest that planthopper populations are threatened by the continuing invasion of brome among cordgrass patches and displacement of native matrix types.

The fitted models as well as direct observation of the planthoppers suggest that a significant fraction of the population was sessile on both cordgrass and brome, at least during the observation period of the experiments (see also Haynes &

Cronin 2006). A possible explanation is that individuals alternate between mobile and sessile states, perhaps between feeding or resting vs. dispersal, and the overall pattern is a mixture of the two types. Feeding dictates a sessile state for planthoppers on cordgrass but would not explain the pattern for brome because it is not a host plant, although individuals could still be resting there. Firle *et al.* (1998) also found that carabid beetles spend large amounts of time in a resting state, and this seems a probable pattern for most dispersing organisms. The combination of sessile and mobile states would generate a leptokurtic pattern of dispersal, with more individuals remaining near the origin than expected based on diffusive movement. Theoretical work suggests that if the organisms exchange frequently enough between dispersal states, however, a dispersal pattern that was initially leptokurtic would eventually resemble diffusion in some cases (Skalski & Gilliam 2003), but not always (Zhang *et al.* 2007). Another possibility is that the planthopper population is divided permanently into several classes of dispersers, ranging from slow to fast. If this were true then we would expect the dispersal pattern to remain leptokurtic over time (Skalski & Gilliam 2000). To distinguish among these different explanations it would be necessary to follow marked planthoppers for a significant portion of the adult stage (several days to a week) and ascertain whether individuals have a fixed or variable diffusion rate.

We note that our experimental design and diffusion models could be adapted readily to other organisms and complex natural landscapes, as long as mass mark–recapture

experiments are possible. The process would involve releasing marked individuals at several points within the landscape and then recording their positions after release. One would then construct an equivalent landscape within the software and solve the diffusion model numerically, eventually obtaining maximum likelihood estimates of the model parameters. The main obstacles to this approach are not computational, but a lack of information on dispersal behaviour in multiple habitats as well as edge behaviour. We note that it is also possible to incorporate population dynamics within this computational framework, including predator-prey or other interactions as well as discrete-time systems (Cronin & Reeve 2005).

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