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Edge behaviour in a minute parasitic wasp

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Summary

1. Changes in the density of an organism near a boundary elements (edge effects) are often thought to be generated by changes in movement behaviour, but in most cases the mechanism underlying these effects is unknown.
2. We quantified the movement behaviour of a minute parasitic wasp, *Anagrus columbi*, in relation to edges in its habitat. This wasp attacks eggs of the planthopper *Prokelisia crocea*, which inhabits a wet prairie ecosystem composed of patches of its host plant prairie cordgrass (*Spartina pectinata*) interspersed within a matrix of mudflat, smooth brome (*Bromus inermis*) and native grasses. Two edge types are common in this system, cordgrass-mudflat and cordgrass-brome.
3. We conducted mark–recapture experiments in which wasps were released at the cordgrass-matrix edge and 50 cm within cordgrass or matrix, for both edge types. The marked wasps were recaptured using a grid of sticky traps. We fitted an advection-diffusion model to these data, yielding estimates of the diffusion rate and advection coefficient for cordgrass and matrix, for each release position and edge type.
4. The spatial distribution of wasps was well-described by the advection-diffusion model. The pattern suggests that marked wasps strongly biased their movements towards the edge when released in matrix, and to a lesser extent when released in cordgrass, while edge releases showed little bias. The advection coefficients were similar for the two edge types, as were the diffusion rates for the three substrates (cordgrass, brome, mudflat). The diffusive and advective components of movement were of comparable magnitude for matrix and cordgrass releases, suggesting equal amounts of directed and random movement.
5. Our results suggest the wasps are attracted to cordgrass patches across short distances, and that bias in their movements may concentrate them at the patch edge. Their edge behaviour is qualitatively different from that of the host insect.
6. The methodology described here could be readily adapted to other systems, where direct observations of movement are difficult but mark–recapture studies are feasible.

Key-words: advection-diffusion models, *Anagrus*, dispersal, edge behaviour, landscape, *Prokelisia*

Introduction

Edge effects are often defined as changes in the density of an organism (or other response variables) in the vicinity of a boundary between two habitat types (Fagan, Cantrell & Cosner 1999; Ries & Sisk 2004, 2008). A variety of patterns have been observed in nature, including positive (an increase in density at the edge), neutral (no response) and negative responses (lower densities at the edge) (Lidicker 1999; Ries & Sisk 2004, 2008; Ewers & Didham 2006). It is clear from population models formulated using reaction-diffusion equations that edge effects and behaviours can influence the persistence of organisms within habitat patches as well as interactions between species (Cantrell & Cosner 1999; Fagan, Cantrell & Cosner 1999).

While edge effects exist in many systems (Ries *et al*. 2004), in most cases the actual mechanism underlying changes in density is unknown, although often assumed to involve changes in the movement of the organisms near the edge. One common formulation of edge behaviour in models involves some form of biased random walk, where the organisms bias their movements at the edge (Schultz & Crone 2001; Ovaskainen 2004; Crone & Schultz 2008; Olson & Andow 2008; Ovaskainen *et al*. 2008; Reeve, Cronin & Haynes 2008; Ries & Sisk 2008). For example, if movements are biased towards the edge from either side, this could generate a positive edge response, whereas if movements are biased away from the edge this could generate a negative one. If movements are biased in one direction only at the edge, this can generate a step-like pattern of density (Ovaskainen & Cornell 2003; Ovaskainen 2004).

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We examine here the edge behaviour of a minute parasitic wasp, *Anagrus columbi* Perkins (Hymenoptera: Mymaridae). This parasitoid attacks eggs of the planthopper *Prokelisia crocea* Van Duzee (Hemiptera: Delphacidae), and inhabits the wet prairie ecosystem found in the North American Great Plains (Cronin 2003a,b). The host for the planthopper is prairie cordgrass (*Spartina pectinata* Link; Poaceae). The spatial distribution of prairie cordgrass is highly fragmented, with patches of cordgrass embedded in a matrix of mudflat, other native grasses, and the exotic grass smooth brome (*Bromus inermis*) (Cronin 2003b, 2007a; Haynes & Cronin 2003; Cronin & Haynes 2004). Two edge types are quite common in this system, cordgrass-mudflat and cordgrass-brome. Previous studies (Cronin 2003a,b) suggested that the distribution of *A. columbi* and parasitism of hosts is influenced by the type of edge. However, no studies have examined how the movement behaviour of this parasitoid in response to patch edges could influence these distribution patterns.

Our approach to quantify edge behaviour for *A. columbi* involves fitting an advection-diffusion model to data from mark–recapture experiments. While advection-diffusion models have been used to describe dispersal in a number of systems (e.g. Banks, Kareiva & Zia 1988; Plant & Cunningham 1991; Corbett & Rosenheim 1996a; Skalski & Gilliam 2000; Jian *et al.* 2008), these generally involve releases from a single point, often in homogeneous space, and were not designed to examine edge behaviour. There are theoretical studies that illustrate how advection and diffusion can combine to determine the distribution of insects with respect to edges in one dimension (Okubo & Kareiva 2001; Tyson, Thistlewood & Judd 2007), but these models were not fitted to dispersal data. Our approach differs from earlier work in that we fit an advection-diffusion model to recapture data from releases at various locations with respect to the edge, allowing us to examine changes in dispersal behaviour with location. We also compare edge behaviour for two edge types (cordgrass-brome and cordgrass-mudflat), and have adapted the advection-diffusion model to calculate time-integrated densities like those generated by traps (Turchin 1998). The use of an advection-diffusion model rather than pure diffusion was suggested by our data, which showed that marked *A. columbi* consistently moved towards the edge, indicating an advection term was needed. The methodology could be readily adapted to other small insects that are difficult to directly observe but can be trapped in some way. The overall objective of this approach is to develop a model for both planthopper (Reeve *et al.* 2008) and parasitoid movements in this landscape, and then explore the effects of movement on the population dynamics in this spatially subdivided system.

Materials and methods

STUDY SYSTEM

Prokelisia crocea is monophagous and the dominant herbivore of prairie cordgrass (Cronin 2003a,b,c). Overwintering first instar nymphs emerge in May, feed on the phloem of cordgrass leaves and mature into adults in June. Eggs are laid beneath the leaf epidermis. By mid-August, a second generation of planthopper adults reaches peak density. *Anagrus columbi* is a facultative specialist of *P. crocea* eggs in our field sites and is a important source of mortality for the planthopper, with parasitism rates averaging 21% (Cronin 2003a,b, 2004, 2007a,b). *Anagrus columbi* also has two generations per year, with the adult stage coinciding with the occurrence of planthopper eggs (Cronin 2007b).

Populations of both species at the cordgrass patch level are quite extinction prone, but extinctions have not been recorded for large cordgrass patches (> 1 ha) and so the population structures of both species are best described as mainland-island metapopulations (Cronin 2003c, 2004). Local patch dynamics are also strongly influenced by the composition of the surrounding matrix (Cronin 2003a, 2004, 2007a; Haynes & Cronin 2004; Cronin & Haynes 2004), with patches surrounded by mudflat having higher densities and lower extinction rates for both species than patches surrounded by brome. Cronin (2007a) concluded that mudflat-embedded patches serve as persistent population sources whereas brome-embedded patches function as extinction prone population sieves.

The matrix-dependent local dynamics of the planthopper can be explained, in part, by their edge behaviour (Haynes & Cronin 2006; Reeve *et al.* 2008). Planthoppers readily cross a cordgrass-brome edge in both directions, but cross the cordgrass-mudflat edge primarily in one direction – from mudflat into cordgrass. Previous studies of *A. columbi* have shown that parasitism rates and wasp density were lower at the cordgrass patch edge than the interior when the bordering matrix was mudflat, but no edge effects were found when the matrix was brome (Cronin 2003a). Experiments on the edge behaviour of *A. columbi* that would reveal the mechanism behind these distributional patterns have not been conducted.

DISPERSAL AND EDGE BEHAVIOUR EXPERIMENTS

We conducted a mark–recapture experiment in July–August, 2006 to quantify the movement and edge behaviour of *A. columbi*. The experiment was conducted within the Kelly's Slough National Wildlife Refuge 16 km west of Grand Forks, North Dakota, USA. The source of *A. columbi* was cordgrass leaves collected from areas with high parasitism and containing parasitoids that were within a few days of adult eclosion. Leaves were maintained for 7–10 days in a state suitable for parasitoid emergence by inserting the basal ends into water-filled tubes (water picks) capped with rubber stoppers. Marking of parasitoids was accomplished by coating leaves with fluorescent powder (Day-Glo Color Corporation, Cleveland, OH, USA) using a small paintbrush (Cronin & Haynes 2004). In laboratory trials, nearly 100% of emerging parasitoids were marked by this procedure (Cronin & Haynes 2004, J. T. Cronin, unpublished data). A subset of 25 leaves was dissected to estimate the potential number of female *A. columbi* that could emerge during the 1 week time period (i.e. hosts bearing a parasitoid showing an adult female body). We focused our study on female parasitoids because they are responsible for reproduction and so the redistribution of the species over time.

We selected large natural cordgrass patches with a distinct boundary with the matrix (either brome or mudflat). For each cordgrass patch, 25 water picks containing two infested leaves each were placed in clusters at the edge, 50 cm into the interior of the cordgrass patch, and 50 cm out into the matrix. The areas of cordgrass and matrix were sufficiently large that these releases were far from any other boundary. Each cluster of infested leaves was coated with a different colour fluorescent powder to allow determination of the origin of the parasitoids. Because *A. columbi* exhibits no direct interference among foragers (Cronin 2003a), the mass release of individuals likely did not affect movement behaviour.

Emerging parasitoids were trapped on transparent 8 × 15 cm acetate sticky traps coated with a thin layer of Tanglefoot (The Tanglefoot Co., Grand Rapids, MI, USA). Traps were fastened to wire stakes with the tops 45 cm above the ground – approximately the same height as the host eggs and where *A. columbi* adults are frequently trapped (Cronin 2003b). Traps were spaced 25 cm apart in a grid pattern that was centred on the edge release site (Figs 1 and 2). The grid dimensions were 200 × 100 cm, with traps extending 100 cm into the patch interior and matrix. Traps were oriented parallel to the cordgrass boundary.

Separate grids were established for three mudflat- and three brome-bordered cordgrass patches. Grids were spaced far enough apart (> 50 m) that movement between them was unlikely (Cronin & Haynes 2004). The grid locations varied in compass direction, reducing the chances for any bias in movement due to orientation with respect to the sun or wind.

The experiment was terminated 1 week after the fluorescent-powdered leaves were placed in the grids. Sticky traps were wrapped in cellophane and the side facing the cordgrass patch interior was marked, and later examined under a microscope at 25–50×. Usually only a few particles of powder were present on each wasp and the three colours were easily distinguishable (Cronin & Haynes 2004). We recorded the number of marked female *A. columbi* caught on each trap side and also the number of unmarked, naturally occurring females. From dissections of the infested leaves, we estimate that an average of 1554 marked parasitoids were released and 90·5 recaptured per grid, for a recapture efficiency of 5·8%.

As the distribution of hosts may also influence the movements of *A. columbi*, we estimated planthopper egg densities in the cordgrass patches associated with each of the six grids. At the edge, and 50 and 100 cm from the edge, five haphazardly chosen cordgrass stems were collected at the end of the study. The leaves were dissected and the number of planthopper eggs per stem were recorded. We tested whether the within-patch distribution of hosts varied with matrix type using profile analysis, with matrix type a fixed effect and replicate grids as subjects, and the three locations within the patch the dependent variables (Simms & Burdick 1988).

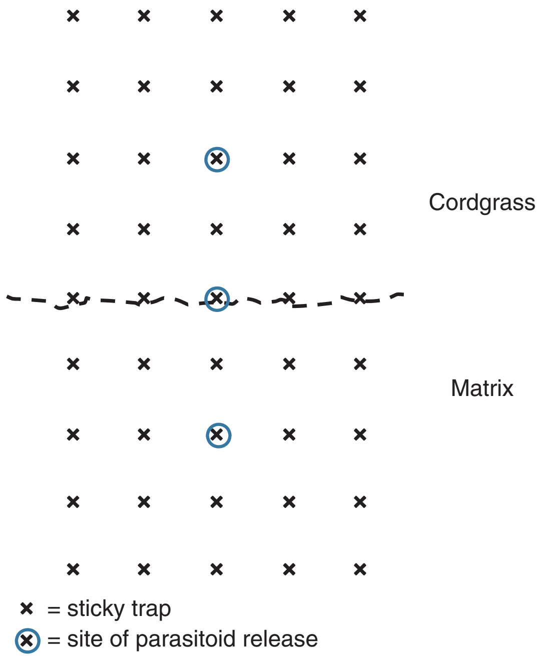

Fig. 1. Diagram showing locations of sticky traps and release points for marked parasitoids in the mark–recapture experiments. Distance between traps is 25 cm.

Fig. 2. Sticky traps and infested leaves with emerging *Anagrus columbi* for a cordgrass-mudflat replicate of the mark–recapture experiment. The plants in the foreground are *Salicornia rubra*, a species sometimes occurring in mudflat.

DIRECTION OF MOVEMENT

We used the centroid of the captured female wasps to determine if there was a net direction of movement from each release point. The data were the (x, y) coordinates of marked wasps on a 5 × 5 array of traps surrounding each release point, treating the release point as the origin. Each trap side was considered a separate observation, separated in space by 1 cm along the y-axis. We then tested whether the centroid was significantly different from (0,0) using a Hotelling-T^2 test (Johnson & Wichern 1998). We combined replicates to increase the sample sizes for these tests, because the data in different replicates appeared similar. MANOVA was used to compare the centroids for brome and mudflat matrix types, with a separate analysis conducted for each release point (matrix, edge, or cordgrass).

ADVECTION-DIFFUSION MODELS

Our centroid results suggested directed movement at right angles to the cordgrass-matrix edge for some release points, but little movement parallel to the edge. We therefore fitted an advection-diffusion model that permitted advection in this particular direction (along the y-axis). Numerical solutions of the model were obtained using COMSOL 3·4 (COMSOL AB 2007). We first defined a landscape that consisted of a 300 × 200 cm rectangle with absorbing boundaries. This rectangle was larger than the 200 × 100 cm region of sticky traps to reduce boundary effects on the model solution. The rectangle was bisected by an interior boundary representing the cordgrass-matrix edge.

We obtained population densities of marked female *A. columbi* by numerically solving the two-dimensional advection-diffusion equation

$$\frac{\partial u}{\partial t} = D_i\left(\frac{\partial^2 u}{\partial x^2}+\frac{\partial^2 u}{\partial y^2}\right) - \beta_i\frac{\partial u}{\partial y} - \delta u \qquad \text{eqn 1}$$

subject to the boundary conditions given above (Reeve *et al.* 2008). Here, u is the density of female wasps, while D_i and β_i are the diffusion and advection rates on each side of the cordgrass-matrix edge ($i = 1$ matrix, $i = 2$ cordgrass). The parameter δ is the disappearance rate of wasps during the experiment. Disappearance can include mortality as well as dispersal not measured by trapping, such as above the plant canopy (Turchin & Thoeny 1993). However, in our system it is most likely due to mortality as few wasps are found above the canopy (K. J. Haynes & J. T. Cronin, unpublished data). Our model also assumes that the dispersing wasps are not significantly depleted by the trapping process, which appears to be true in our experiments (only 5·8% were recaptured). See Yamamura *et al.* (2003) for an alternate approach when depletion occurs. We also attempted fitting a model using a biased random walk for edge behaviour (Ovaskainen 2004), the same behaviour successfully used for the host planthopper (Reeve *et al.* 2008). This model did not provide an adequate fit and was not further considered.

We assumed a mean life span for adult females wasps of 1 day ($\delta = 6{\cdot}944 \times 10^{-4}$ min^{-1}) based on previous studies (Cronin 2003a,b), although we checked other values (see Results). The initial distribution of insects was modelled as a bivariate normal ($\sigma = 2$ cm) density multiplied by a scaling parameter α (to be estimated from the data) centred on each release point. This scaling parameter will likely be influenced by the number of wasps released as well as trap efficiency. We used $\sigma = 2$ cm because it gives a narrow initial distribution of wasps, approximating a point release as used in analytical dispersal models. Although smaller values can be used they increase the time needed for numerical solutions.

Although the above procedure yields the wasp density at a given point in time and space, the trap data are not in this form because they integrate the density of insects over time. To obtain a time-integrated density c, we added the equation $\frac{dc}{dt} = u$ to the COMSOL model, assuming $c = 0$ at $t = 0$. We solved the combined model from $t = 0$ until $t = 5760$ min (4 days), a period sufficient for nearly all wasps to die or disperse from the trapping grid.

Maximum likelihood was used to estimate the diffusion model parameters, assuming the number of wasps on a trap was Poisson with mean $\mu = c$, where c is the time-integrated density of wasps (see also Yamamura 2002). The log likelihood function was the sum of the log Poisson probabilities for each trap, assuming the traps are independent observations. Each trap side was again considered a different observation, separated in space by a small distance (1 cm) along the y-axis. This convention was useful for traps on the cordgrass-matrix boundary, with the different sides considered to lie in either cordgrass or matrix. We used the simplex algorithm (Nelder & Mead 1965) as implemented in MATLAB 7·5 (The MathWorks Inc. 2007) to minimize $-\log L$ as a function of the model parameters. A MATLAB driver program contained the routines for minimizing the likelihood, calling COMSOL as needed to solve the advection-diffusion equation.

We combined replicate grids of traps to increase the sample size for parameter estimation, yielding six data sets, one for each of the three release points in cordgrass-mudflat and cordgrass-brome arenas. This pooling seemed appropriate because the spatial pattern of captures were similar across replicates, as was the number recaptured ($\overline{Y} = 30{\cdot}2, s = 15{\cdot}3$). We deleted the traps closest to each release point because wasps were less likely to encounter them after emergence (they were located directly above the release point), leaving a total of 264 trap sides in each data set. We fitted three models to each data set with differing assumptions: (i) equal diffusion and advection rates in cordgrass and matrix ($D_1 = D_2$, $\beta_1 = \beta_2$), (ii) equal diffusion rates but different advection rates ($D_1 = D_2$, β_1, β_2 free to vary), (iii) different diffusion rates but equal advection rates (D_1, D_2 free to vary, $\beta_1 = \beta_2$). We then compared the fit of the different models using AIC values (Burnham & Anderson 2002). Models involving different diffusion rates were never the best-fitting models, and were not further considered. We calculated approximate 95% confidence values for the parameters in model (1) by inverting a likelihood ratio test for each parameter (Bickel & Doksum 1977). We also generated plots for this model of the mean observed vs. expected number (± SE) of female *A. columbi* for each row of traps along the y-axis. An R^2-value using the mean observed and expected frequencies was also calculated.

SPATIAL DISTRIBUTION OF UNMARKED PARASITOIDS

We used Poisson regression to examine the distribution of unmarked *A. columbi*, with matrix type and trap location along the y-axis the main effects in the model (preliminary analyses showed little variation along the x-axis). Each trap side was treated as a separate observation. We first fitted a model that included a matrix type × y location interaction, which was non-significant, and so fitted a reduced model containing only main effects. A random effect of replicate (nested within matrix type) was also included in the model. The models were fitted using PROC GLIMMIX in SAS 9.1 (SAS Institute Inc. 2003). Pairwise differences in female *A. columbi* densities among trap locations were examined using Tukey's method for Poisson regression (SAS Institute Inc. 2003).

Results

The centroids for marked female wasps differed significantly from the origin (the release point) for matrix releases (both types) and cordgrass, but were non-significant for edge releases (Table 1). Examination of the centroid values suggests movement was primarily along the y-axis, perpendicular to the cordgrass-matrix edge. Female wasps released in both matrix and cordgrass appeared to move towards the edge. There were no significant differences between the centroids for brome vs. mudflat matrix types, for releases in matrix ($F_{2,71} = 1{\cdot}60$, $P = 0{\cdot}209$), at the edge ($F_{2,89} = 0{\cdot}92$, $P = 0{\cdot}402$), and within cordgrass ($F_{2,67} = 0{\cdot}58$, $P = 0{\cdot}560$).

The fitted advection-diffusion model echoed the pattern for the centroids, with positive values of β observed for matrix releases, negative ones for cordgrass releases, and relatively small values for edge releases (Table 1). The β values were significantly different from zero for all matrix and cordgrass releases (using 95% confidence intervals), while the edge release was significant only for cordgrass-mudflat arenas (β was positive indicating movement towards the cordgrass interior). This pattern was also visible in plots of the observed and expected numbers of insects, because the peaks for both matrix and cordgrass releases were shifted towards the edge (Fig. 3). This figure also shows the estimated distances traveled in 1 day through advection alone, calculated from these β values. R^2-values for the fitted models ranged from 0·651 to 0·940 (Table 1).

Models assuming equal advection rates in cordgrass vs. matrix generated lower (better) AIC values than models

Table 1. Centroids and parameter estimates for releases of marked *Anagrus columbi* at three locations near a cordgrass-matrix edge

Matrix	Release	Wasps	Centroid	D (cm^2 min^{-1})	β (cm min^{-1})	α	R^2	AIC$_1$	AIC$_2$
Mud	Matrix	99	(−0·35, 30·32)***	0·410	$3{\cdot}88 \times 10^{-2}$	10·09	0·651	351·20	344·82
95% CI	Lower			0·252	$2{\cdot}72 \times 10^{-2}$	8·19			
	Upper			0·783	$6{\cdot}39 \times 10^{-2}$	12·35			
Brome	Matrix	89	(−4·03, 19·71)***	0·561	$3{\cdot}52 \times 10^{-2}$	9·30	0·750	361·80	363·62
95% CI	Lower			0·326	$2{\cdot}36 \times 10^{-2}$	7·45			
	Upper			1·224	$6{\cdot}26 \times 10^{-2}$	11·80			
Mud	Edge	84	(−1·62, 9·38)	0·653	$1{\cdot}23 \times 10^{-2}$	7·29	0·940	286·50	288·24
95% CI	Lower			0·344	$3{\cdot}86 \times 10^{-3}$	5·65			
	Upper			1·781	$3{\cdot}33 \times 10^{-2}$	9·94			
Brome	Edge	13	(−5·59, 3·59)	1·495	$1{\cdot}08 \times 10^{-2}$	12·21	0·736	394·70	390·84
95% CI	Lower			0·701	$-3{\cdot}45 \times 10^{-3}$	8·99			
	Upper			9·480	$7{\cdot}18 \times 10^{-2}$	37·60			
Mud	Cordgrass	96	(−1·44, −21·88)***	0·284	$-1{\cdot}73 \times 10^{-2}$	9·85	0·911	346·24	345·54
95% CI	Lower			0·190	$-2{\cdot}49 \times 10^{-2}$	7·92			
	Upper			0·464	$-1{\cdot}25 \times 10^{-2}$	12·30			
Brome	Cordgrass	62	(−8·33, −19·17)***	0·577	$-2{\cdot}93 \times 10^{-2}$	5·98	0·734	278·60	280·58
95% CI	Lower			0·306	$-6{\cdot}00 \times 10^{-2}$	4·54			
	Upper			1·555	$-1{\cdot}79 \times 10^{-2}$	8·07			

Listed are the number of marked wasps trapped, centroids for these wasps using the release point as the origin, and parameter estimates for a fitted advection-diffusion model assuming equal diffusion (D) and advection (β) rates on cordgrass vs. matrix, with α a scaling parameter. R^2-values were calculated using the mean observed and expected densities of wasps (see Fig. 3). Also shown are AIC values for this model (AIC$_1$) and one permitting different advection rates for cordgrass and matrix (AIC$_2$).
***$P < 0{\cdot}001$, Hotelling-T^2 test.

allowing different advection rates for half the data sets (Table 1). The differences in AIC values were small except for wasps released in mudflat, where the different advection rates model provided a better fit. The estimated advection rates here were $\beta_{\text{matrix}} = 5{\cdot}35 \times 10^{-2}$, $\beta_{\text{cordgrass}} = 1{\cdot}53 \times 10^{-2}$, suggesting rapid movement from mudflat towards cordgrass and then a slower rate within cordgrass. We also fitted models using a smaller value of the disappearance (mortality) rate δ ($\delta = 3{\cdot}472 \times 10^{-4}$ min^{-1}), implying a mean adult life span of 2 days (twice the 1 day default). This change yielded estimates of β, D, and α half those in Table 1, and we conclude these parameters scale with δ as they do in simpler models with disappearance and time-integrated data (Turchin & Thoeny 1993).

The distribution of unmarked, naturally occurring female wasps (Fig. 4) varied significantly with trap location ($F_{8,526} = 4{\cdot}75$, $P < 0{\cdot}0001$) while the matrix effect was non-significant $F_{1,4} = 0{\cdot}11$, $P = 0{\cdot}762$). Multiple comparisons across trap locations suggested that wasp densities were highest from 0 to 75 cm (the edge to 75 cm inside the cordgrass patch), but were significantly lower for some matrix traps and the 100 cm cordgrass trap (Fig. 4).

The distribution of hosts did not differ between patches bordered by brome or mudflat ($F_{1,4} = 0{\cdot}12$, $P = 0{\cdot}742$). Regardless of matrix type, planthopper eggs per stem at the patch edge, and 50 and 100 cm into the cordgrass interior were statistically indistinguishable (position: $F_{2,3} = 1{\cdot}44$, $P = 0{\cdot}365$; position × matrix type: $F_{2,3} = 4{\cdot}21$, $P = 0{\cdot}135$), averaging 56·61 ± 2·95 eggs (based on grid means, $n = 6$).

Discussion

Our centroid and advection coefficient results both suggest that female *A. columbi* moved towards the edge when released in either cordgrass or matrix, regardless of the matrix type. For releases at the patch edge, there was also significant advection towards the patch interior when the matrix was mudflat but not brome. The pattern observed in unmarked, wild individuals suggests an increase in female *A. columbi* density close to the patch edge, perhaps generated by these edge behaviours.

Would the edge behaviours we observed help retain *A. columbi* within cordgrass patches? We can assess this from the model parameters by calculating the distances moved by advection or diffusion during the 1 day (1440 min) life span of the adult wasps. Given the β values in Table 1, we would expect that wasps would travel *c.* 50 cm ($\beta \times t$) through advection during their life span for matrix releases, with lesser distances for other locations. Using the average D value from Table 1 ($\overline{D} = 0{\cdot}663$ cm^2 min^{-1}), we would expect a root-mean-squared displacement of about 62 cm ($\sqrt{4Dt}$) through diffusion alone. These values suggest a rough equity between the two processes, with advection concentrating the wasps near the patch edge and opposing the tendency of diffusion to spread the population. This is the pattern predicted in theoretical studies where advection and diffusion terms act in opposition (Okubo & Kareiva 2001; Tyson *et al.* 2007) at an edge. Without an opposing advection term, we would expect that wasps would be lost by diffusion from cordgrass patches, especially the smaller-sized ones ($< 0{\cdot}5$ m^2) that are quite common (Cronin 2003c, 2004). Our results for the

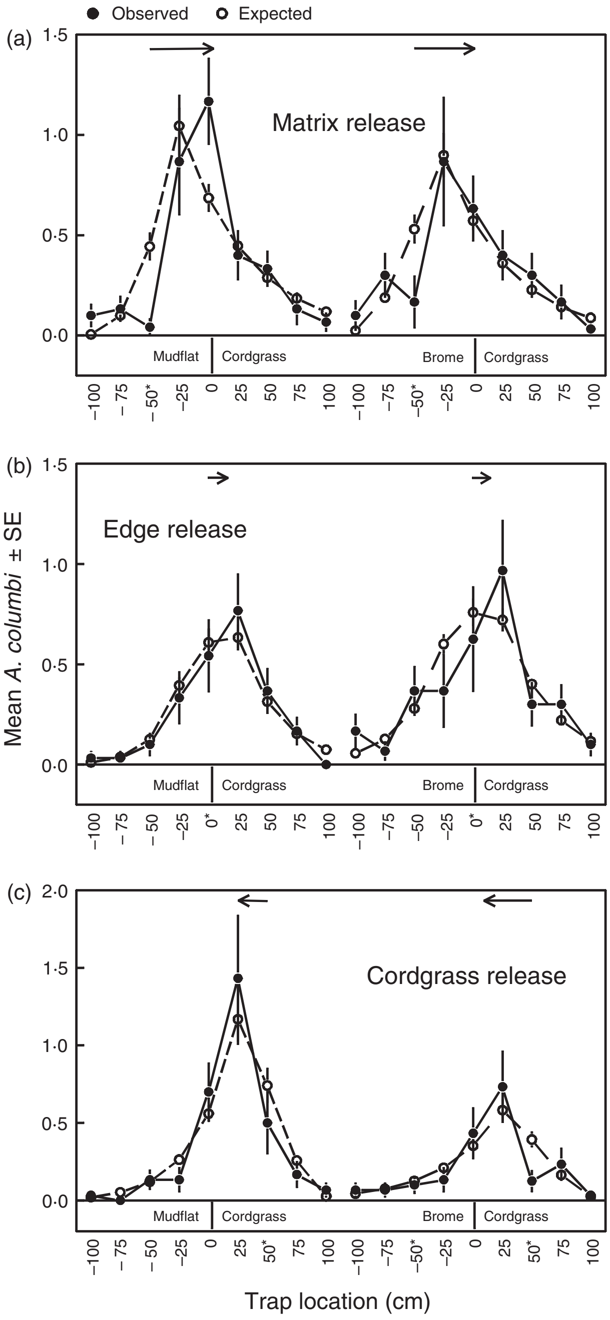

Fig. 3. Mean observed and expected frequencies (±SE) of marked *Anagrus columbi* at trap locations extending from the cordgrass-matrix edge (0 cm) into the cordgrass patch (25, 50, 75 and 100 cm) or the matrix (−25, −50, −75 and −100 cm). The expected frequencies were generated using a advection-diffusion model fitted to the trap data (see Materials and Methods). The release points are denoted with an asterisk. Arrows indicate the magnitude and direction of advective movement from the release point, assuming a 1 day life span.

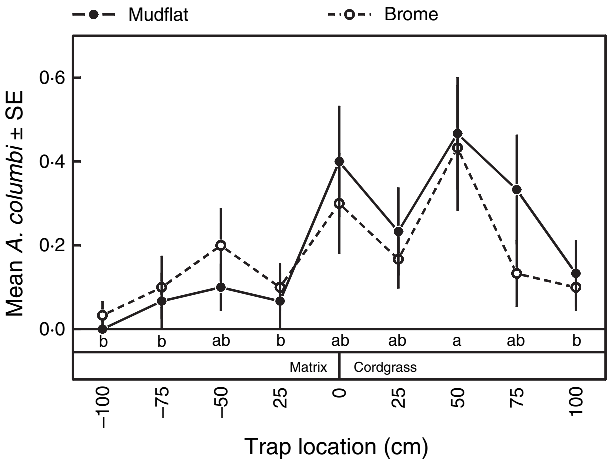

Fig. 4. Mean frequencies (±SE) of unmarked, naturally occurring *Anagrus columbi* at trap locations extending from matrix into cordgrass, for mudflat and brome matrix types. Trap locations with different letters are significantly different (Tukey's method).

advection process also implies that wasps are attracted to cordgrass patches across short distances in the matrix, at least 50 cm. However, it is important to note that the distances calculated here are average, not maximum, distances. *Anagrus columbi* has been captured dispersing as far as 30 m in mudflat and 50 m in brome from its emergence site (Cronin 2003a; Cronin & Haynes 2004). It seems likely that *A. columbi* dispersal is a mixture of short-range, somewhat directed movements and long-distance ones possibly aided by the wind, as reported for other parasitoid species including other *Anagrus* (e.g. Corbett & Rosenheim 1996b; Cronin & Strong 1999; Compton *et al.* 2000; Henne, Johnson & Cronin 2007).

Why might adult female *A. columbi* move towards the edge of a cordgrass patch? Wasps seeking hosts would be expected to move towards cordgrass from the matrix, but there was also significant movement from cordgrass towards the edge of the patch. Previous studies have indicated higher nitrogen levels in edge plants for both matrix types (Haynes & Cronin 2003), and for cordgrass patches adjoining mudflat, planthopper adult densities were higher at the edge than interior. The related species *A. nilaparvatae* responds to plant volatiles released by planthopper feeding (Lou, Ma & Cheng 2005) and can also distinguish among rice varieties (Lou *et al.* 2006), so it is plausible that *A. columbi* is responding to differences in the volatiles released by edge plants. However, independent studies found no edge effect with regard to host egg densities (Cronin 2003a; this study) or cordgrass stem densities (Cronin 2003a; K. J. Haynes and J. T. Cronin, unpublished data), so it appears unlikely that *A. columbi* is moving to the patch edge in response to increased host encounter rates or the concentration of plant volatiles. It may be that the cordgrass edge has a more suitable microclimate or lower predator densities (such as mirid bugs that feed on *Prokelisia* eggs; Finke & Denno 2002) than the patch interior. Another possibility is that larger, more nutritious eggs are produced by *P. crocea* feeding on nitrogen-rich edge plants, and these are preferred by *A. columbi.* Numerous studies have shown that parasitoids are quite selective about host size (e.g. Reeve 1987; Karamaouna & Copland 2000; Lin & Ives 2003).

Our results appear at odds with previous work that indicates matrix type has a very strong effect on the local persistence and density of *A. columbi* populations (Cronin

2003a), with patches surrounded by mudflat being significantly more likely to persist and have higher densities than patches in brome. Also, *A. columbi* has almost a tenfold higher rate of dispersal between patches embedded in brome than in mudflat. Based on these data, we expected to see stronger advection terms for mudflat releases relative to brome (in the direction of the cordgrass), or edge behaviours similar to those observed for the host insect (see below). However, the estimated advection-diffusion parameters were similar for the two matrix types.

We offer an alternative explanation for the differences in patch level dynamics of *A. columbi* in mudflat- vs. brome-bordered patches that fits with our findings that this wasp exhibits little matrix-dependent difference in edge behaviour. First, lower rates of dispersal between patches in mudflat relative to patches in brome could be explained by higher rates of dispersal mortality in mudflat. Mudflats tend to be somewhat hotter and drier and lacking in shade relative to brome habitats (Cronin & Haynes 2004). Also, without vegetation to block winds these minute insects may have their movements impeded or be driven off course. Second, *A. columbi* may have higher densities and persist longer in mudflat-embedded patches simply because its host shows that pattern. The main predictor of adult *A. columbi* density is host density (Cronin 2003a,b, 2004, 2007a; Cronin & Haynes 2004). We have regularly detected a matrix effect on *A. columbi* density or persistence independent of host density, but it often accounts for a small proportion of the model variance ($<10\%$ as compared to $>50\%$). The significant advection that female *A. columbi* displays at the cordgrass-mudflat edge, and potentially high dispersal failure in the mudflat matrix, could be sufficient to generate an independent matrix effect. One lesson to be learned here is that although patterns of abundance and distribution can provide clues regarding movement behaviour, there is no substitute for explicit movement experiments.

There appear to be substantial differences in edge behaviour between *A. columbi* and its host, the planthopper *P. crocea*. Edge behaviour in adult *P. crocea* was investigated using a design similar to this study, except that the planthoppers were directly observed (Reeve *et al*. 2008). One difference between host and parasitoid are the magnitudes of the advection and diffusion rates. The diffusion rate for the adult planthopper was roughly twice that of *A. columbi* for cordgrass and brome, and eight times higher for mudflat, but there was no obvious advection component. Another difference involves the nature of the edge behaviour, which was well-described in the planthopper by a biased random walk formulation that generates a step-like pattern in density at the edge (Ovaskainen & Cornell 2003; Ovaskainen 2004; Ovaskainen *et al*. 2008). We were unable to obtain satisfactory fits for this model for *A. columbi*, and in any event the densities appeared continuous at the edge (Fig. 3). The planthopper also exhibited stark differences in its behaviour for brome vs. mudflat matrix, unlike *A. columbi*. In particular, adult planthoppers readily crossed from mudflat to cordgrass but not in the opposite direction, while movements were more symmetrical for cordgrass and brome (Haynes & Cronin 2006; Reeve *et al*. 2008). One cause of these differences may be different methods of locomotion – flight for *A. columbi* vs. walking from leaf to leaf in the planthopper. A cordgrass-mudflat edge likely represents a more distinct edge for the planthopper than the parasitoid, involving a descent to ground level when leaving the cordgrass patch.

Although there is a substantial literature on how landscape context affects parasitoid abundance, parasitism rates, and species richness (e.g. Marino & Landis 1996; Maron & Harrison 1997; Roland & Taylor 1997; Doak 2000; Kruess & Tscharntke 2000; Tylianakis, Didham & Wratten 2004; Elzinga *et al*. 2005; Roth, Roland & Roslin 2006; de Almeida, Wirth & Leal 2008; Cronin 2009), we note there is almost no information on how parasitoid movement is affected by landscape features, including movement rates in habitat patches vs. matrix and how these organisms respond to edges. Yet, some understanding of parasitoid movements will be required to understand landscape patterns in parasitism rates and parasitoid abundance, because they are generated by parasitoid and host movement in combination with local population dynamics (Roth *et al*. 2006). Information on both these processes will also be needed to explain host-parasitoid dynamics at a landscape level (Cronin & Reeve 2005). We hope the methodology presented here will prove useful in quantifying edge behaviour and movement for these organisms.

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