Movement, colonization, and establishment success of a planthopper of prairie potholes, *Delphacodes scolochloa* (Hemiptera: Delphacidae)

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Abstract. 1. Movement, and particularly the colonisation of new habitat patches, remains one of the least known aspects of the life history and ecology of the vast majority of species. Here, a series of experiments was conducted to rectify this problem with *Delphacodes scolochloa* Cronin & Wilson, a wing-dimorphic planthopper of the North American Great Plains.

2. The movement of brachypterous and macropterous planthoppers within and among host-plant patches was quantified. Also, an experiment was conducted to assess whether planthopper propagule size (i.e. number of colonists) influenced the presence of planthopper adults or eggs over time, planthopper population growth rate (R_0), and abundance or impact of an egg parasitoid.

3. *Delphacodes scolochloa* movement was well described by a simple diffusion model. As expected, brachypters were less dispersive than macropters – mean displacement distances among patches were three times greater for macropters (2.8 m vs. 8.1 m per day).

4. Number of colonists of vacant patches increased with increasing patch size (both wing forms) and decreased with increasing isolation (brachypters only). At the scale of individual potholes ($<$38 m), brachypters were dispersal limited.

5. Establishment success was strongly influenced by propagule size. An Allee effect constrained the establishment of new populations, but low establishment success was not a result of mate limitations or the presence of natural enemies (i.e. egg parasitoids).

6. These movement data reveal important insights regarding the spatial population structure and spread of *D. scolochloa*.

Key words. Allee effect, mark-release-recapture, mating status, parasitism, *Scolochloa festucacea*, spatial spread, wing dimorphism.

Introduction

For subdivided populations, movement is a key process influencing local and regional dynamics, population spread, species interactions, and local adaptation (Hanski, 1999; Holyoak *et al.*, 2005). Interpatch dispersal is a critical determinant of colonization–extinction dynamics in metapopulations and metacommunities (Hanski, 1999; Holyoak *et al.*, 2005; Schtickzelle *et al.*, 2007). Sink habitats may be able to sustain a population through a constant influx of individuals from nearby source habitats (Holt, 1985; Pulliam, 1988; Kawecki, 2004). Population

spread is contingent upon both trivial and long-distance dispersal events (Hengeveld, 1989; Shigesada *et al.*, 1995; Johnson *et al.*, 2006). Coexistence of predator–prey and inter-specific competitor interactions can depend on the relative rates of dispersal (Horn & MacArthur, 1972; Comins *et al.*, 1992; Nee & May, 1992; McCauley *et al.*, 1996; King & Hastings, 2003). Finally, spatial population structure and local adaptation are promoted by reduced dispersal among patches (Nagylaki, 1975; Wright, 1978; Hanks & Denno, 1994; Whitlock, 2002). Despite the voluminous literature on each of these subjects, movement remains one of the least known aspects of the life history and ecology of the vast majority of species (Turchin, 1998).

There has been a long history of study of insect movement using mark-release-recapture experiments (Turchin, 1998); although, lepidopterans, coleopterans, and dipterans have

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received the most attention (Cronin, 2003). Hemimetabolous insects, such as grasshoppers, planthoppers and leafhoppers, have scarcely been studied (but see With & Crist, 1995; Kindvall, 1996; Briers & Warren, 2000; Cronin, 2003). In the vast majority of cases, the redistribution of individuals was generally well fit by simple diffusion models (Kareiva, 1983; Turchin, 1998). However, in the few cases where it has been considered, a better model fit is provided by relaxing the assumption that all individuals diffuse at the same rate (Okubo, 1980; Cronin *et al.*, 2000; Yamamura, 2002). This added realism accounts for the leptokurtosis (fat-tailed distribution) often detected in recapture-with-distance data, and gives appropriate weight to long-distance dispersal events (Turchin, 1998). Differences in wing morphologies, limb lengths or body sizes are likely contributors to this dispersal heterogeneity (e.g. Cronin *et al.*, 2000). In the case of wing-dimorphic species, differences in dispersal between brachypterous (short-winged) and macropterous (long-winged) individuals is almost always inferred (e.g. Denno *et al.*, 1991; Roff & Fairbairn, 1991; but see Socha & Zemek, 2003).

The geographical variables patch size and isolation are considered to be of overriding importance in determining the likelihood of an immigration or colonisation event (Hanski, 1999). The vast majority of empirical studies support the idea that immigration increases with patch size and decreases with increasing isolation (Hanski, 1999). In contrast, establishment success (i.e. the likelihood that offspring will be left behind by a colonist) is by far the least understood and experimentally studied aspect of dispersal. Establishment success can depend on the number of colonists or on the propagule size (Grevstad, 1999; Lockwood *et al.*, 2005; Memmott *et al.*, 2005; Drake & Lodge, 2006), the mating status of the immigrant or the ability of the immigrant to find mates once it has arrived (Hopper & Roush, 1993; Fauvergue *et al.*, 2007). The failure to find mates is thought to be a major cause for an Allee effect, or a positive relationship between per-capita growth rates and population density (Hopper & Roush, 1993; Drake & Lodge, 2006). Demographic stochasticity, particularly strong in small founding populations, may also adversely affect establishment success (Lande, 1998). Finally, other common factors that may hinder establishment are the presence or subsequent colonisation of competitors or predators in the patch (e.g. Morin, 1984; Losos & Spiller, 1999; Resetarits, 2001). In order to understand patterns of patch occupancy and the spread of natural and invasive species, studies are needed that assess the factors which limit colonisation and establishment success (Ims & Yaccoz, 1997; Drake & Lodge, 2006).

A series of experiments was conducted to quantify the movement, colonisation behavior, and establishment success of *Delphacodes scolochloa* Cronin & Wilson (Hemiptera: Delphacidae), a wing-dimorphic planthopper found in prairie potholes of the North American Great Plains (Cronin & Wilson, 2007). A mark–recapture experiment was conducted for brachypterous and macropterous females to test whether wing morphs differed in the scale or pattern of within-patch movement, or if their redistribution in space is well described by simple or heterogeneous diffusion models. A second experiment was conducted to test whether the number of immigrants to vacant host–plant patches was influenced by patch size or isolation. In that study, the mating status of immigrants was ascertained.

Finally, an experiment was conducted to assess whether the number of females released onto isolated patches influenced the presence of planthopper adults or eggs in subsequent censuses, per-capita growth rate of the planthopper, and abundance or impact of an egg parasitoid.

Materials and methods

Study system

The prairie pothole region of the North American Great Plains is a formerly glaciated area characterised by numerous seasonal and permanent ponds or potholes (van der Valk, 1989). A dominant wetland plant associated with these potholes is the native grass, sprangletop [*Scolochloa festucacea* (Willd.) Link; Poaceae: Pooidae; Smith, 1973]. Sprangletop often encircles pothole margins, or occurs as smaller patches (<5 m^2) in the open water of shallow potholes (Cronin & Wilson, 2007).

The planthopper *D. scolochloa* is an abundant specialist herbivore of sprangletop (Cronin, 2007, 2008; Cronin & Wilson, 2007). Planthoppers overwinter as nymphs in the senescent leaf sheaths. In early May, nymphs emerge and begin feeding and reach peak adult densities at the end of May. A second generation follows, with maximal adult densities occurring in the middle of July. All of the adult males and $< 10\%$ of the adult females are macropterous and capable of sustained flight (Cronin & Wilson, 2007). Brachypterous females have small wing buds that limit them to dispersing predominantly by walking and hopping. Median lifespan of an adult female in the laboratory is only 6 and 5 days for brachypters and macropters, respectively (Cronin & Wilson, 2007). In the field, adult life spans appear to be approximately one-half as long (Cronin, 2007, 2008).

Eggs are inserted beneath the stem epidermis and are parasitised by two fairyfly parasitoids, *Anagrus nigriventris* Girault and A. *columbi* Perkins (Hymenoptera: Mymaridae; Cronin, 2007, 2008; Cronin & Wilson, 2007). *Anagrus nigriventris* is the dominant egg parasitoid accounting for 92% of the parasitised hosts. Due to the difficulty in distinguishing these minute parasitoids, they were treated as one in this study. Over the course of six generations, parasitism of *D. scolochloa* eggs was $21.7 \pm 4.2\%$ (Cronin, 2007).

Within-patch movement

A mark-release-recapture study was conducted to characterise the pattern and rate of adult planthopper movement within monospecific patches of sprangletop. Adult planthoppers were captured with sweepnets from potholes in Nelson County, North Dakota (48.02097°N, 98.12230°W). Planthoppers were sorted by sex and wing form and then quickly transported on ice to the release site. Planthoppers were then lightly dusted with fluorescent powder (Day-glo Color Corporation, Cleveland, OH) and gently released into the centre of a large sprangletop patch (≥ 20 m radius). As planthoppers warmed up, they began walking and only rarely took flight; thus, an escape response was not evident (Cronin, 2007). In addition, fluorescent powders do not

appear to adversely affect planthopper survivorship or dispersal (J. T. Cronin, unpubl. data; see also Cronin, 2003). Planthoppers never exhibited an escape response after their release.

Twenty-four hours after the release of marked planthoppers, a D-vac vacuum insect sampler (Rincon-Vitova, Ventura, CA) with a 0.085 m² head was used to recapture dispersing insects. Samples were obtained from concentric circles at distances of 0.5 m ($n = 2$ samples), 1.0 m ($n = 4$), 2.0 m ($n = 8$), 4.0 m ($n = 16$), 8.0 m ($n = 22$), and 12.0 m ($n = 26$) from the release point. Suction samples were 5 s in duration and were spaced an equal distance apart within an annulus. For each distance, the mean number of recaptures per sample was converted to a density; i.e. the number/m². Six replicate releases were performed using brachypterous females and ambient proportions of males. Two additional releases were conducted using macropterous females (and ambient proportions of males). For these releases, the most distant sampling locations were set at 20 m ($n = 60$). The number of marked female planthoppers varied from 100 to 600, which allowed for a test of whether release density influenced planthopper redistribution. Due to the scarcity of males, only females were used in subsequent analyses. Each release was conducted on a separate day and within a different sprangletop patch. Based on stem counts obtained from 12 haphazardly chosen locations within each of the eight patches (using 0.25 m × 0.25 m sampling frame), there were no significant differences among patches in mean number of stems per m² ($F_{7,88} = 0.46$, $P = 0.86$).

The density distributions of planthoppers 24-h post-release was compared with the predictions of two models of diffusion: a simple model based on the Gaussian distribution that assumes a homogeneous population of dispersers (Okubo, 1980) and a more complicated model that accounts for heterogeneity in diffusion rates (Cronin *et al.*, 2000). In the simple diffusion model, N_r is the expected density of planthoppers at distance r, and is determined from the formula:

$$N_r = Ye^{-\frac{r^2}{Z}}$$

Y is the scaling parameter and Z is the dispersion parameter and is equal to $-4Dt$; where D is the diffusion rate and t is the time since release (Turchin, 1998). The fit of the diffusion model to the density distributions of *D. scolochloa* was evaluated with least-squares regression using the linear form of the diffusion model, $\ln(N_r) = \ln(Y) - r^2/Z$. Here, as the slope of the relationship between $\ln(N_r)$ and r^2 becomes more negative (slope $= -1/Z$), the rate of diffusion decreases. The model fit was determined from the coefficient of variation (R^2). Finally, the estimates of Y and Z were used to generate the expected distribution of planthoppers, from which the standard deviation σ and 50% ($= 0.67\sigma$) and 95% ($= 1.96\sigma$) quantiles were computed. These quantiles represent the radius of a circle r that is expected to contain that proportion of marked planthoppers.

Deviation from the predictions of simple diffusion commonly occurs in the form of a leptokurtic density distribution; i.e. lower-than-expected recaptures near, and greater-than-expected recaptures farther away from the source (Turchin, 1998; Cronin *et al.*, 2000). Leptokurtosis is likely to arise when the population is heterogeneous in its dispersal ability, as might be found when the population consists of both fast and slow dispersing individuals

(Okubo, 1980; Turchin, 1998). Here, the heterogeneous diffusion model is the summation of two simple diffusion models (Cronin *et al.*, 2000):

$$N_r = Y_1 e^{-\frac{r^2}{Z_1}} + Y_2 e^{-\frac{r^2}{Z_2}}$$

where Y_1 and Y_2 and Z_1 and Z_2 are the scaling and dispersion parameters, respectively, for the two types of dispersers. The fit of the heterogeneous model to the combined data for each wing type was assessed using non-linear regression in SYSTAT 12.0 (Systat Software, Inc., San Jose, CA). If the heterogeneous diffusion model provides a better fit to the density distribution of planthoppers, the 95% CI of Z_1–Z_2 should not overlap zero.

Colonisation behaviour

The effects of patch isolation and size on *D. scolochloa* immigration to vacant patches (colonization) was assessed by de-faunating sprangletop patches and then capturing immigrants derived from a large mainland source population. Three large potholes (0.4–1.2 ha) were selected from Nelson County that had a discrete patch of sprangletop (area of 132–724 m²) along one portion of the shoreline (Fig. 1). The vegetation bordering the remainder of the pothole was either cattail (*Typhus* sp.) or sedge (*Scirpus* sp.). Extending into the shallow water were discrete sprangletop patches that varied in size from 0.01 m² to 12.5 m² and in isolation from the source by 0.9 m–38 m. All patches were surrounded by a water or bare-mud matrix. The total number of patches was 45 (22, 11, 12 per pothole). No other sprangletop was within 65 m of these patches.

At the midpoint of the adult period (late May), planthopper adults and nymphs were removed from these patches by repeatedly vacuuming with a D-vac. Every day for 5 days, after the de-faunation of patches, the patches were thoroughly vacuumed to collect planthopper colonists. Colonists from each patch were transferred to plastic bags, returned to the laboratory, and the
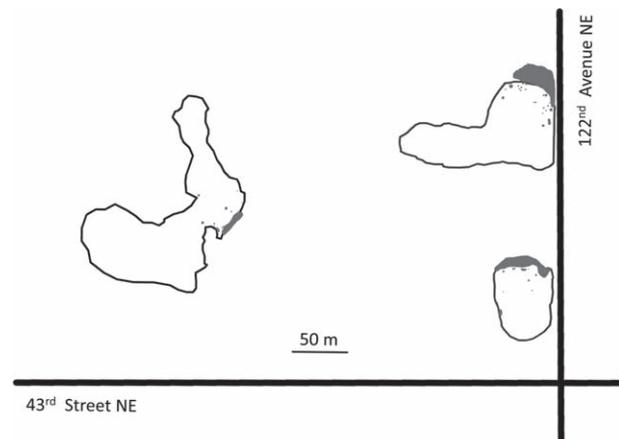
Fig. 1. Map of three potholes used in the colonisation behaviour study. Pothole perimeters and sprangletop patches (dark objects) were mapped using a Leica Geostystems System 500 GPS with Coast Guard beacon receiver (sub-meter accuracy). Study site was located in Petersburg, North Dakota.

number of males and females of each wing type recorded. For patches containing female but no male colonists in the day's collection, females were transferred to individual cages on sprangletop stems to evaluate mating status. The stem cage was constructed from a 10 cm long by 2.5 cm diameter acetate tube. High-density foam sealed the ends of the tube around the stem. After 2 weeks, the cage was removed and the stem dissected. The presence of eggs with developing eye spots was used as evidence that females were mated. This is a conservative estimate of mating status, because some of the females may have failed to oviposit or develop mature embryos for reasons other than a lack of sperm in their spermatheca. Moreover, using females captured from male-free patches, this approach minimised the likelihood that matings took place after colonisation. For comparison, females were also collected each day from the mainland and tested for mating status. A total of 83 and 102 caged females from the islands and mainland, respectively, were used in this study.

The effects of patch size and isolation on immigration were evaluated with a generalised linear mixed model using Proc GLIMMIX in SAS 9.1.3. As the number of colonists per patch was Poisson distributed, the data distribution in the model was set as Poisson. Pothole was treated as a random-block effect and the continuous independent variables, patch size and isolation, were each *ln*-transformed prior to analysis. Separate tests were performed for males, brachypterous females and macropterous females.

The difference in the proportion of females that were macropters on the mainland versus islands, was assessed with a χ^2-test. In addition, separate χ^2-tests were performed to determine if the proportion of macropters and proportion of females producing viable young varied with distance from the mainland. Distances were divided into categories (<2 m, 2–5.9 m, 6–16 m, >16 m) to ensure that all cells within the contingency table had a sample size ≥ 5.

Establishment success

The effect of propagule size and parasitism on the establishment success of *D. scolochloa* was assessed by releasing different densities of female planthoppers (brachypters or macropters) onto experimental patches of sprangletop, placed either near or far from mainland sources of *Anagrus* egg parasitoids. The experiment was conducted at two potholes in Nelson Co., North Dakota and at the tail end of the adult planthopper period (mid July, second generation). A patch consisted of a potted clump of sprangletop (30-cm diameter) placed in a water-filled pan. Based on previous studies (Cronin, 2007, 2008), *D. scolochloa* and *Anagrus* respond similarly to experimental and similarly sized natural patches. Egg-laying rates by planthoppers and patterns of parasitism by *Anagrus* were similar between the two types of patches.

Sprangletop patches were excavated when planthoppers were in the early nymphal stages and the pots ($n = 220$) were spaced 10 m apart and positioned >50 m away from any naturally occurring sprangletop (within a matrix habitat predominated by the grasses *Bromus inermus* and *Hordeum jubatum*). This pro-

cedure minimised the colonisation of patches by non-experimental planthoppers and parasitoids. One week prior to the release of planthoppers, all patches were sprayed with insecticidal soap to eliminate all herbivorous insects.

Planthoppers were collected with a sweepnet and only adult female brachypters were used in the experiment. Planthoppers were transported on ice to the experimental potholes, marked with fluorescent powder and released at one of five propagule sizes (1, 2, 4, 16 or 32 per pot) within 2 h of their capture. Planthoppers were counted 20 min later and missing individuals were replaced. At each pothole, the lowest three density levels were replicated 20 times each. The 16 and 32 females/pan treatment levels were replicated 16 and 10 times, respectively. For comparison, patches with 1, 2, 4, and 16 macropterous female propagules were also set up at the same time (replication per treatment level was one-half that for the brachypterous females). The highest propagule treatment was omitted because of the relative rarity of macropters. Finally, during the collection of planthoppers, a sample of females ($n = 35$) was returned to the laboratory and assayed for mating status. Patches were inspected at 8 h and then twice daily for 4 days. The number of marked and unmarked (colonising) individuals was counted and all unmarked individuals were removed by hand. At the end of day 4, when almost all planthoppers had either died (see section on Study system) or dispersed, the few remaining individuals were removed from the patches.

To assess the role of *Anagrus* in affecting planthopper establishment success (brachypters only), one half of the pots for each propagule treatment level was placed at 3 m, and the other one half placed at 25 m, from a large mainland patch of sprangletop (containing the primary source of *Anagrus*). Based on a previous study by Cronin (2007), an isolation distance of 25 m is sufficient to greatly reduce number *of Anagrus* colonists. Pots were moved 3 days after planthopper removal to allow time for all planthopper eggs to mature to a stage suitable for parasitoid oviposition (see Cronin & Wilson, 2007). By this date, adult planthoppers were scarce, and if any were detected during twice daily examinations of pots, they were removed.

Pots were spaced 3 m apart. One small sticky trap [4×6 cm acetate sheet coated with Tanglefoot (The Tangletrap Co., Grand Rapids, MI) and mounted on a 25 cm wire stake] was placed in each pot and used to estimate the density of female *Anagrus* (see Cronin, 2007). Traps were left in pots for 1 week, which constitutes the period in which *D. scolochloa* eggs would be vulnerable to parasitism (Cronin, 2007, 2008). Three weeks after the release of planthoppers, all stems with planthopper oviposition scars were collected. In the laboratory, stems were dissected under a stereoscopic microscope ($10\times$). At this time, all healthy hosts should have emerged as nymphs. All hosts were counted, including cast chorions (emerged nymphs), parasitised individuals, and dead eggs. The net replacement rate for planthopper females released onto a patch (R_0) was computed as the number of emerged nymphs divided by the number of propagules per patch. Therefore, this measure takes into account losses in offspring production attributed to egg parasitism and other sources of egg mortality. The proportion parasitised was determined as the number parasitised divided by the total number of host eggs (excluding dead eggs). Finally, an index of

the per-capita number of hosts parasitised per patch was computed, as the total number of hosts parasitised divided by the number of female *Anagrus* captured per patch (see Cronin, 2007).

Separate generalised linear mixed models were used to examine the effects of propagule size (brachypters only), isolation distance, and site (fixed block effect) on planthopper adult female occupancy at different time periods after release, the presence of eggs laid at the end of the experimental period, number of eggs laid per female released onto the patch, R_0, number of immigrant *Anagrus*, proportion of host eggs parasitized, and the per-capita number parasitised. SAS GLIMMIX was used with distribution = normal for parasitism (arcsine-square root transformed), distribution = binomial (logit link function) for presence/absence of adults or eggs, and distribution = poisson for all other variables (log link function). A separate logistic regression analysis was conducted to test whether macropterous or brachypterous females differed in the likelihood of patch occupancy at different time intervals. Wing form was treated as a fixed effect in this model. Finally, differences among propagule levels in the proportion of individuals remaining on a patch were assessed with a non-parametric Kruskal–Wallis test. For all analyses, differences among propagule treatment levels were assessed using Tukey's test on least-square's means.

Results

Within-patch movement

The redistribution of brachypterous female planthoppers after their release within large homogenous sprangletop patches, was well described by a simple diffusion model (Table 1, Fig. 2). With the exception of one of the smallest releases (Trial 109 A), the model fit was quite high ($R^2 \geq 0.81$). For that release, only one female was captured beyond the first set of traps (0.5 m). If that trial 109 A is excluded, the slope of the relationship between *ln* recapture density and squared distance from the release point did not change as release density increased (slope = 0.040, $R^2 = 0.30$, $n = 5$, $P = 0.20$; see Table 1). In fitting the heterogeneous diffusion model to the combined data (excluding Trial 109A; Fig. 2), Z_1–Z_2 was not significantly different from zero (95% CIs: −103.6, 86.0). There was insufficient heterogeneity in brachypterous female diffusion rates to accept this model as a description of their redistribution. Based on the linear model, the 50% and 95% quantiles for dispersal were 1.25 and 2.13 m, respectively (Table 1). Macropterous female movement was also well described by Gaussian diffusion (Table 1; $R^2 > 0.65$), and the data were not better fit by a heterogeneous diffusion model (95% CIs for Z_1–Z_2: −25.81, 26.51). The radius of a circle containing 50% or 95% of dispersers was 58% greater for macropters than brachypters (Table 1). The greater diffusion rate for the former morph is evident in the flatter slope in Fig. 2 (slope ± SE; brachypters: −0.035 ± 0.007; macropters: −0.011 ± 0.003).

Colonisation behaviour

For the sprangletop patches in the open water of prairie potholes, the number of colonists from the mainland increased significantly as patch size increased for males and females of both wing forms (Table 2, Fig. 3). In all cases, the number of colonists declined with increasing isolation distance, but the effect was only significant for brachypterous females ($P < 0.001$; Table 2). There was no evidence that patch size and isolation interacted to affect colonisation (Table 2). The mean displacement of brachypterous females was 2.8 ± 0.2 m ($n = 213$), and was approximately three times less than the mean displacement of macropterous males and females [8.0 ± 0.5 m ($n = 249$) and 8.1 ± 1.0 m ($n = 98$), respectively]. The difference was statistically significant (Tukey's pairwise comparison test, $P < 0.001$).

Table 1. The fit of a simple Gaussian diffusion model to the density distribution of separate releases of brachypterous and macropterous female planthoppers. Time since release was 24 h. Marked is the number of fluorescent-marked females per release and Slope is derived from the relationship between the squared distance from the release and *ln* number of recaptures per m². The coefficients of determination (R^2) and associated *P*-values are also presented, along with the maximum distance captured (MaxDist) and dispersal quantiles (estimated radius of a circle enclosing 50% or 95% of the dispersers; in metres).

Replicate	Marked	Slope	R^2	P	MaxDist	Dispersal quantiles 50%	95%
Brachypters							
100B	150	−0.114	0.848	0.026	4	1.19	2.02
109A	150	−0.337	0.298	0.454	8	0.91	1.54
100A	300	−0.055	0.878	0.021	8	1.42	2.43
109B	300	−0.124	0.812	0.037	4	1.16	1.98
100C	600	−0.060	0.883	0.005	8	1.39	2.40
109C	600	−0.059	0.883	0.006	8	1.40	2.39
Mean ± SE		−0.12 ± 0.04	0.77 ± 0.09	0.09 ± 0.07	6.7 ± 0.8	1.25 ± 0.08	2.13 ± 0.14
Macropters							
100C2	100	−0.018	0.770	0.009	12	1.88	3.21
100C3	175	−0.012	0.525	0.066	20	2.08	3.54
Mean		−0.015	0.65	0.04	16.0	1.98	3.38
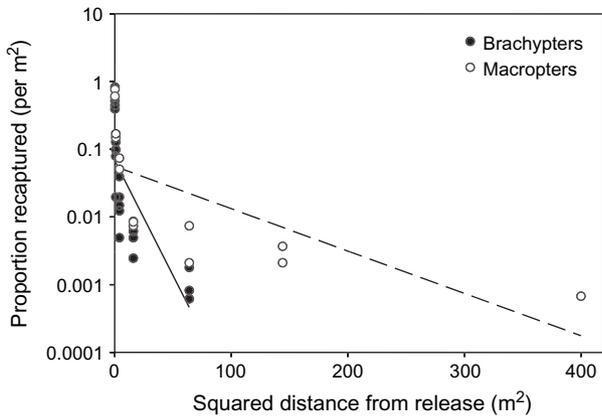
Fig. 2. The density distributions of brachypterous (closed circle) and macropterous (open circles) females 24 h after their release in monospecific patches of sprangletop. Lines were fit by least-squares regression for the combined data from five brachypterous and two macropterous trials, and represent the fit of the data to a simple Gaussian diffusion model. Brachypters: $R^2 = 0.528$, $n = 28$, $P < 0.001$; macropters: $R^2 = 0.52$, $n = 14$, $P = 0.004$.

The proportion of females that were macropters in the mainland was 0.08 ($n = 381$ females), but the proportion was 3.4 times greater for all colonists combined ($\chi^2 = 49.0$, d.f. = 1, $P < 0.001$). Among patches, this proportion increased significantly with distance from 0.19 for patches <2 m to 0.85 for patches >16 m from the mainland ($\chi^2 = 51.1$, d.f. = 3, $P < 0.001$). Laboratory oviposition trials revealed that 87% of the colonist females produced viable young. Brachypterous and macropterous females did not differ in this regard ($\chi^2 = 0.43$, d.f. = 1, $P = 0.51$). In addition, the mating status of colonists was no different than for females collected at large from the mainland (94% in the latter habitat; $\chi^2 = 2.98$, d.f. = 1, $P = 0.142$).

Establishment success

Number of adult female propagules strongly influenced the likelihood that the patch was occupied and received eggs. At 8 h, 30% of the patches receiving one brachypterous female were occupied (Fig. 4a). Occupancy rates increased significantly and levelled off to close to 100% when the propagule size was ≥16 per pot ($F_{4,162} = 4.25$, $P = 0.003$). Results were similar for the 1,

2 and 3 days time periods (not shown). In addition, the proportion of released brachypters that remained on the patch after 8 h increased from 32% to 40% from a propagule size of one to 32, but the effect was not statistically significant ($\chi^2 = 5.26$, d.f. = 3, $P = 0.154$; Fig. 4b). Based on a subsample of females, 86% (30 of 35 individuals) were capable of producing viable offspring in laboratory trials. Finally, the likelihood that a patch was oviposited in by brachypterous females mirrored that of the 8 h occupancy rates ($F_{4,162} = 63.61$, $P = 0.008$).

Macropterous females exhibited occupancy rates at 8 h that were significantly lower than the rates for brachypters ($F_{1,219} = 4.63$, $P = 0.033$; Fig. 4A). This difference was most evident at the lowest propagule size treatment, in which occupancy rates were three times higher for brachypters. Wing morph did not interact with propagule size to affect occupancy rates ($F_{3,219} = 0.08$, $P = 0.97$; Fig. 4a). Finally, the proportion of macropters that remained on the patch at 8 h increased by almost threefold from a propagule size of 1 to 16 ($\chi^2 = 5.55$, d.f. = 3, $P = 0.0136$; Fig. 4b).

The per-capita number of eggs laid by brachypterous planthoppers exhibited a humped-shaped relationship with respect to propagule size (Fig. 5a, Table 3, $P < 0.001$). Maximum number of eggs laid occurred at a propagule size of four females. Propagule number also had a significant positive effect on R_0 ($F_{4,161} = 18.62$ $P < 0.001$), but isolation distance also affected R_0 through its interaction with propagule number (isolation: $F_{1,161} = 0.01$ P 0.905; propagule number*isolation: $F_{4,161} = 5.08$ $P < 0.001$). At a distance of 25 m, R_0 increased with propagule number up to four individuals per patch, and then levelled off at approximately five nymphs per female (Fig. 5b). In contrast, at 3 m, R_0 exhibited a humped-shaped response to propagule number (Fig. 5b). An average of 2.3 nymphs per female was produced at the highest propagule number; less than half the value for planthoppers on the 25-m isolated patches.

The number of female *Anagrus* colonising each patch averaged 5.04 ± 0.3 and 1.84 ± 0.20 at 3 m and 25 m, respectively (a significant difference; Table 3, $P < 0.001$). Planthopper propagule size had no effect on parasitoid colonists ($P = 0.831$; Fig. 5c). As expected, the proportion parasitised per patch was significantly higher for patches nearer the mainland source (0.20 ± 0.2 vs 0.12 ± 0.02 for the 3-m and 25-m patches, respectively; Table 3, Fig. 5d). Parasitism also increased significantly with propagule size (Table 3, $P < 0.001$; Fig. 5d). This pattern was more evident in the 3-m than 25-m patches, but no interaction between propagule size and isolation was evident. Finally, the per-capita number of hosts parasitised increased significantly

Table 2. Results from separate Poisson regression analyses for the effect of patch size (m²), patch isolation (m), and pothole (random block effect) on number of *Delphacodes scolochloa* colonists. Reported are *F*-statistics and *P*-values (in parentheses). *P*-values in bold were deemed statistically significant after controlling for the experiment-wise error rate associated with three non-independent tests (based on a Bonferroni-corrected level of α).

Independent variables	Num/Den DF	Planthopper type		
		Males	Female Brachypters	Female Macropters
Isolation	1, 39	2.87 (0.098)	**119.35 (<0.001)**	4.17 (0.048)
Size	1, 39	**48.56 (<0.001)**	**67.09 (<0.001)**	**24.68 (<0.001)**
Isolation*size	1, 39	0.62 (0.436)	0.74 (0.394)	0.67 (0.418)
Pothole	2, 39	0.07 (0.937)	0.68 (0.513)	1.24 (0.301)

(a)

(b)

(c)
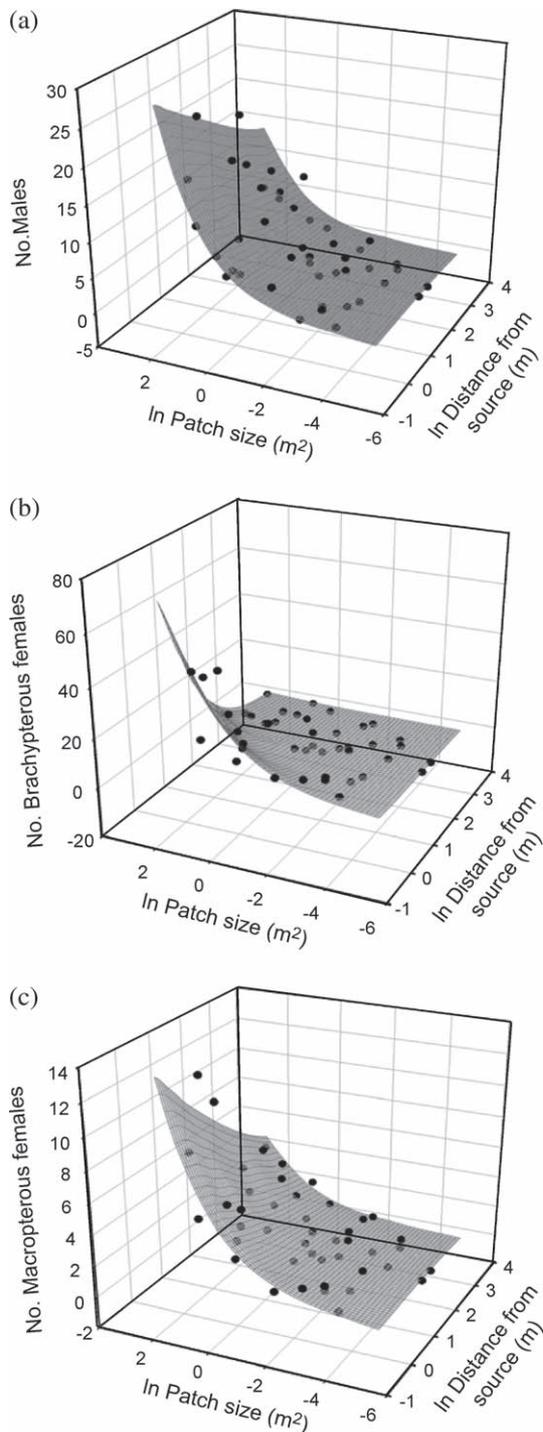
Fig. 3. Relationship between patch size and patch isolation on the number of (a) male, (b) brachypterous female, and (c) macropterous female colonists. The surface is based on predicted values derived from separate Poisson regression analyses performed in SAS GLIMMIX.

with increasing propagule size, but was unaffected by isolation distance (Table 3, Fig. 5e). However, there was a strong interaction between propagule size and isolation distance on the per-
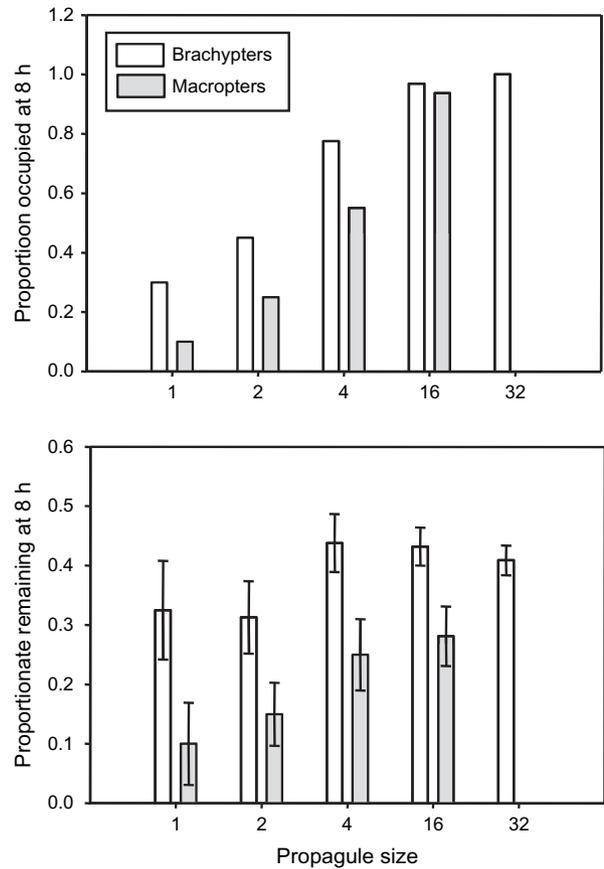
Fig. 4. Effect of propagule size on the (a) proportion of patches that were occupied 8 h later, and (b) mean ± SE proportion of propagules released into the patch that were present 8 h later. Brachypterous and macropterous females are represented by clear and grey bars, respectively.

capita parasitised – nearby patches had the highest per-capita parasitised at the lowest propagule size, but isolated patches had the highest per-capita number at the highest propagule size (Table 3, Fig. 5e). Interestingly, the per-capita parasitised decreased with increasing parasitoid density, although the relationship was not quite statistically significant ($P = 0.015$; Table 3). Finally, arthropod predators, primarily spiders, were scarce in all experimental bus pans, irrespective of isolation distance or propagule size.

Discussion

This series of experiments revealed much regarding the movement of *D. scolochloa*, and provides a necessary foundation for deciphering the spatial and temporal dynamics of these highly-fragmented planthopper populations. The movement behaviour of *D. scolochloa* within and among host-plant patches is typical of many other insect species that live in fragmented landscapes (Turchin, 1998; Hanski, 1999). *Delphacodes scolochloa* movement within relatively homogeneous sprangletop patches was very well fit by a simple diffusion model; explaining 65% and
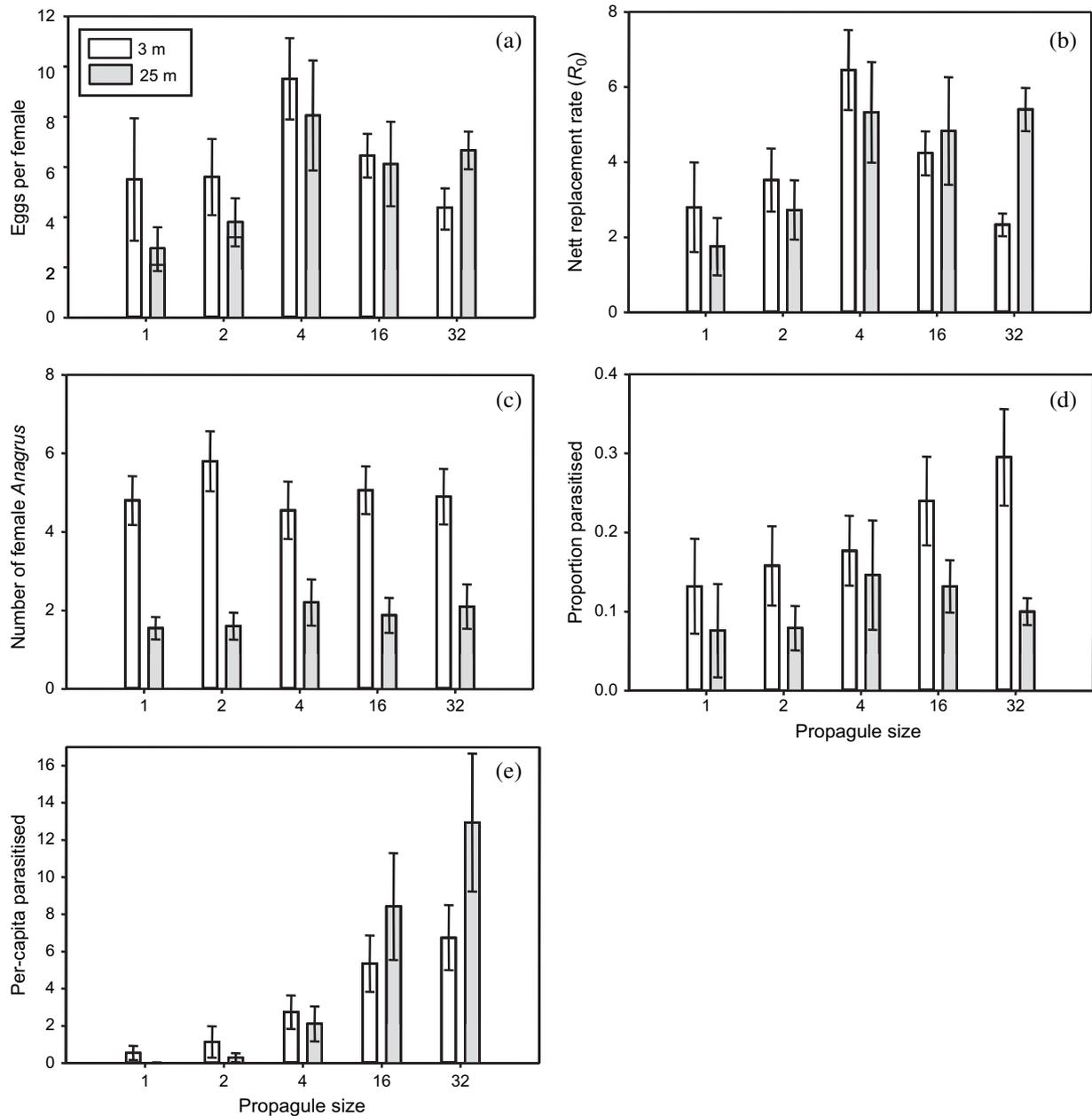
Fig. 5. Effect of propagule size on (a) number of eggs laid per female planthopper, (b) planthopper growth rate over one generation (R_0), (c) number of female Anagrus colonists, (d) the proportion of hosts parasitised by *Anagrus*, and (e) the per-capita number of hosts parasitised by *Anagrus*. Patches placed at 3 m and 25 m away from a source of insects are represented by clear and grey bars, respectively. Means ± SE are reported.

77% of the variance in recaptures for macropterous and brachypterous females, respectively.

Macropterous females had a diffusion rate that was 58% higher and a mean net displacement among patches that was almost three times higher (2.8 m vs 8.1 m) than brachypterous females. These differences do not seem extraordinary given the fundamental differences in dispersal capabilities of the two wing morphs (Cronin & Wilson, 2007). The distance traversed by walking/hopping versus flying might be expected to differ by

an order of magnitude or more. However, such quantitative data on the differences in dispersal for wing-dimorphic species is quite rare (e.g. Socha & Zemek, 2003) and almost always inferred (e.g. Denno *et al.*, 1991; Roff & Fairbairn, 1991).

In this study, the fit of the diffusion model to the redistribution of a mixture of females of both wing morphs (at natural proportions) was not evaluated. However, the threefold greater diffusion rate for macropters than brachypters (based on a comparison of slopes; see Table 1) is likely to generate leptokurtic

Table 3. Statistical results for the effects of propagule size, isolation density, and site on number of eggs per female planthopper, planthopper net replacement rate (R_0), *Anagrus* colonists per patch, proportion of hosts parasitised, and the per-capita number of hosts parasitised. Parasitism was analysed with standard ANOVA methods and all other response variables were analysed using Poisson regression (see Methods). Site ($n = 2$) was treated as a fixed block effect and *Anagrus* density (*ln*-transformed) was used as a covariate in the analysis of per-capita parasitism. *P*-values in bold were deemed statistically significant after controlling for the experiment-wise error rate associated with four non-independent tests (based on a Bonferroni-corrected level of α).

Dependent variable	Num DF	Eggs per Female	R_0	*Anagrus* density	Proportion parasitised	Per-capita parasitised
				Response variables		
Propagule size*	4	**28.15 (<0.001)**	**18.72 (<0.001)**	0.37 (0.831)	**8.47 (<0.001)**	**54.49 (<0.001)**
Isolation	1	1.18 (0.279)	0.01 (0.905)	**108.1 (<0.001)**	**14.02 (<0.001)**	3.08 (0.083)
Propagule*Isolation	4	2.04 (0.091)	**5.08 (<0.001)**	1.26 (0.288)	0.24 (0.871)	**7.21 (<0.001)**
Site	1	1.36 (0.246)	1.34 (0.249)	3.42 (0.0066)	0.01 (0.980)	**17.03 (<0.001)**
Anagrus density	1	—	—	—	—	6.08 (0.015)
Denom. DF			161	161	123	92

*For proportion and per-capita parasitism, the initial density $= 1$ treatment level was omitted from the analysis because only a small percentage of patches had host eggs.

redistribution curves that are indicative of a higher-than-expected number of long-distance dispersers (Okubo, 1980; Cronin *et al.*, 2000; Yamamura, 2002). Heterogeneous diffusion rates could arise from many causes, including differences in wing or locomotory morphology, body size, sex, mating status, reproductive state, age, and nutritional state (e.g. Davis, 1984; Cronin *et al.*, 2000; Bellamy & Byrne, 2001; Coll & Yuval, 2004; Bancroft & Smith, 2005). In recent years, human-assisted transport has received much attention as a source of leptokurtic dispersal curves (e.g. Aubry *et al.*, 2006; Johnson *et al.*, 2006; Henne *et al.*, 2007). For example, the transportation of gypsy moth eggs by automobiles contributes significantly to the rate and pattern of spread of this pernicious pest (Johnson *et al.*, 2006).

In support of the expectations of island biogeographic and metapopulation theory, and the existing empirical evidence (Table 9.1; Hanski, 1999), the number of *D. scolochloa* colonists (males and females of either wing type) increased with increasing patch size. At the scale of this study (patch isolation $\leq$38 m), brachypterous females, the predominant wing morph, showed strong evidence of dispersal limitation, and its effect was stronger than the patch-size effect. Number of macropter colonists also declined with isolation, but the effect was not quite statistically significant. If the scale of this study was expanded from the movement within to among potholes (in which isolation distances are typically an order of magnitude greater; see Fig. 1), dispersal limitation in macropters would probably be evident. The importance of macropters to long-distance dispersal is clearly evident, when examining the proportion of females that are macropters in the samples collected from the mainland and isolated patches. From the mainland to patches <2 m away, the proportion of macropters more than doubled (0.08 to 0.19). It more than quadrupled between > 2 m and $\geq$16 m (0.85).

A substantial body of literature, particularly with invasive species (e.g. Lockwood *et al.*, 2005; Memmott *et al.*, 2005; Drake & Lodge, 2006), has revealed that propagule pressure is one of the most important predictors of establishment success. Propagule pressure is also tied to the spread of invasives, as high propagule size can overcome Allee effects at the invasion front that might otherwise pin the population to its current location

(Keitt *et al.*, 2001; Johnson *et al.*, 2006; Tobin *et al.*, 2007). In agreement with these studies, patch occupancy and likelihood of eggs being laid by *D. scolochloa* increased significantly as the number of adult females per patch increased. There was also strong evidence of an Allee effect in these experimental populations – R_0 increased with propagule size, reaching a maximum at a density of four females per patch. Contrary to expectations (Hopper & Roush, 1993; Drake & Lodge, 2006), the Allee effect likely was not the result of limited mates available at low density, because *D. scolochloa* females had a high probability of being mated (87% of all immigrants). Clearly, pre-dispersal mating would be advantageous in highly fragmented habitats, as even a single-founding individual may be able to establish a population.

The Allee effect in *D. scolochloa* appeared to be caused, in part, by the low probability that any individuals remained on the patch after 8 h when the propagule size was low. Only 30% and 10% of the patches with 1–2 brachypters and macropters, respectively, were occupied at 8 h, and the proportion of individuals remaining on the patches at 8 h tended to increase by 25% for brachypters and 180% for macropters from the lowest to the highest propagule size. Kuussaari *et al.* (1998) found similar results for the Glanville fritillary. Why *D. scolochloa* may have a proclivity for conspecifics is not known. However, at low to moderate densities, the presence of conspecifics could lead to improved protection against predators (e.g. Turchin & Kareiva, 1989; Aukema & Raffa, 2004), increased ability to overcome host defences (e.g. Young & Moffett, 1979; Wallin & Raffa, 2004), improved nutrient acquisition (e.g. Cook & Denno, 1994; Wise *et al.*, 2006), or provide cues about host or patch quality (e.g. Donahue, 2006).

Natural enemies can cause or contribute to an Allee effect if prey mortality decreases with increasing prey density (inverse density dependence), or they can counteract an Allee effect if prey mortality increases with increasing prey density (density dependence; Courchamp *et al.*, 1999; Keitt *et al.*, 2001). For parasitoids, inverse density-dependent parasitism and direct density-dependent parasitism have been reported with equal frequency in the literature (Walde & Murdoch, 1988). In this

study, as propagule size decreased, *Anagrus* per-capita parasitised and proportion parasitised decreased. Thus, if anything, the action of *Anagrus* parasitoids may serve to weaken the existing Allee effect. The likelihood of discovery of patches by *Anagrus* did not depend on host density, and even when parasitoids were abundant (*cf.* patches at 3 m versus 25 m from the source), parasitism was low in low density host patches. *Anagrus* appears to be relatively ineffective in sprangletop patches newly colonised by a small number of hosts. In contrast, patches receiving a high propagule number were more heavily parasitised (see Fig. 5d), which contributed to the low R_0 at nearby (3-m) patches.

Despite density-dependent parasitism of hosts, the mean proportion of hosts parasitized did not exceed 30%. Parasitoid interference, in which the per-capita number of hosts parasitised tended to decline with increasing parasitoid density (Hassell, 2000), may have aided in preventing *Anagrus* parasitism from reaching a level so high that host establishment was certain to fail. Interference, which has been reported for several species of *Anagrus* (Cronin & Strong, 1993; Cronin, 2003), may also have explained why the per-capita number parasitised at 25 m was higher than at 3 m (when host densities were high).

In summary, *D. scolochloa* is generally dispersal limited, even at the scale of within prairie potholes. Macropterous individuals are likely to be the only link among potholes, but given the rarity and modest vagility of these long-winged morphs, potholes are likely to have relatively low connectivity. Planthopper populations distributed among the ensemble of potholes that characterise the northern Great Plains may be functionally independent (see Harrison & Taylor, 1997; Thomas & Kunin, 1999). Colonisation of new patches is more likely if patches are large and isolation distances are small. Upon colonising a new sprangletop patch, establishment success was strongly influenced by propagule size. An Allee effect constrained the establishment of new populations from few founding individuals, but low establishment success was not because of mate limitations or the presence of natural enemies. Given the generally short dispersal distances and Allee effects operating in this system, the spread of *D. scolochloa* would probably be gradual (see Johnson *et al.*, 2006).

Acknowledgements

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