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Individually mark–mass release–resight study elucidates effects of patch characteristics and distance on host patch location by an insect herbivore

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Abstract. 1. How organisms locate their hosts is of fundamental importance in a variety of basic and applied ecological fields, including population dynamics, invasive species management and biological control. However, tracking movement of small organisms, such as insects, poses significant logistical challenges.

2. Mass-release and individual–mark–recapture techniques were combined in an individually mark–mass release–resight (IMMRR) approach to track the movement of over 2000 adult insects in an economically important plant–herbivore system. Despite its widespread use for the biological control of the invasive thistle *Carduus nutans*, the host-finding behaviour of the thistle head weevil *Rhinocyllus conicus* has not previously been studied. Insects were released at different distances from a mosaic of artificially created host patches with different areas and number of plants to assess the ecological determinants of patch finding.

3. The study was able to characterize the within-season dispersal abilities and between-patch movement patterns of *R. conicus*. Weevils found host plant patches over 900 m away. Large patches, with tall plants, situated close to the nearest release point had the highest first *R. conicus* resights. Patch area and plant density had no effect on the number of weevils resighted per plant; however, *R. conicus* individuals were more likely to disperse out of small patches and into large patches.

4. By understanding how *R. conicus* locates host patches of *C. nutans*, management activities for the control of this invasive thistle can be better informed. A deeper mechanistic understanding of host location will also improve prediction of coupled plant–herbivore spatial dynamics in general.

Key words. *Carduus nutans*, host patch location, mark–release–recapture, patch area, patch characteristics, plant density, *Rhinocyllus conicus*.

Introduction

Dispersal ability, host plant location and patch choice are crucial drivers of herbivore distributions (Grez & Gonzalez, 1995; Cronin *et al.*, 2001; Bowman *et al.*, 2002). Understanding patterns and mechanisms of host location by insect herbivores is of interest for both basic and applied ecology (Catton *et al.*, 2014). The distribution of host plants can influence herbivore densities (Tsafack *et al.*, 2013) and the effects of these herbivores on host plant growth and survival (Hahn & Orrock, 2015), and thus can also influence the effectiveness of biocontrol agents (Schneider *et al.*, 2015). Due to the ephemeral nature of its habitat, an insect may emerge as an adult in a location where its host plant is no longer present. In such circumstances, being able to move and locate a suitable host plant, using appropriate cues (e.g. visual or olfactory), is critical for survival. Once a host plant patch has been located, an insect must also assess the quality of the host plant patch (for purposes of feeding, reproduction or refuge) and decide to either stay within that patch or to continue moving. Together, these processes generate resulting distribution patterns, but unfortunately, many studies focus only on the distributional outcomes and fail to describe the movement behaviour that creates the observed patterns (Kareiva,

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1982; Bach, 1988). Inferring pattern from process is challenging at best, and impossible when data do not allow discrimination of alternative hypotheses about generative processes.

Studying insect movement is non-trivial because of difficulties in marking individuals without detrimental effects, balancing the often conflicting challenges of resighting individuals, measuring a diffusive process with discrete measures (by tracking sufficient individuals), and determining spatial scales that are relevant to the species (Clobert *et al.*, 2001; Hagler & Jackson, 2001; Bowler & Benton, 2005; Skarpaas *et al.*, 2005; Holden, 2006; Skarpaas & Shea, 2007; Jongejans *et al.*, 2008, 2015). Mass–mark–release (MMR) studies are commonly used to estimate how far insects move (Kareiva, 1982, 1985; Osborne *et al.*, 2002), but individual movement cannot be studied. In contrast, individually mark–release–recapture (IMRR) studies are often used for estimating population densities, but can also provide great insight into individual movement behaviours in complex environments (Lebreton *et al.*, 1992; Petit *et al.*, 2001; Schneider *et al.*, 2003). For example, tracking individual behaviour provides insights about dispersal into and out of a patch as affected by patch characteristics such as patch area, plant abundance and plant density (Kareiva, 1985). IMRR is logistically challenging, however, particularly when individuals must be captured, marked and released individually.

We combined these two mark–release approaches (MMR and IMRR) into an individually mark–mass release–resight study (IMMRR), utilising benefits of both methods. We investigate the movement, host location and subsequent distribution of the thistle head weevil *Rhinocyllus conicus* (Frölich), an introduced biocontrol agent, in response to the spatial distribution of its invasive host, the musk thistle (*Carduus nutans* L.). Prior to *R. conicus*'s original release in the USA in 1969, there was a lack of information on the movement abilities of the weevil across heterogeneous landscapes, which resulted in poor predictions of its probability of colonising remote sites (Louda *et al.*, 2003a). After its introduction, *R. conicus* was observed to have established at a distance of 1.6 km in the first 3 years after its release in Virginia (Kok & Surles, 1975), and 0.6 km in 2 years in Georgia (Buntin *et al.*, 1993). These documented movement rates provide no information on the ecological context of host-finding by the weevil, and how *R. conicus* weevils locate their host plants is also unknown. Visual cues may be involved, and there is some suggestion that olfactory cues are important (Z. Sezen, unpublished); this also provides little insight into the distances over which weevils may locate their hosts. A deeper understanding of its movement may help to explain the weevil's variable success as a biocontrol agent (Kok & Surles, 1975; Rees, 1977; Surles & Kok, 1978; Sheppard *et al.*, 1994; Kelly & McCallum, 1995; Shea & Kelly, 1998; Shea *et al.*, 2005). Specifically, the mass release portion of our IMMRR study was intended to provide more insight into the host-finding abilities of *R. conicus* over longer distances, while the individual marking portion simultaneously allows us to determine individual movement once within a host patch. We thus determined the dispersal abilities, host location and between-patch movement patterns of adult *R. conicus* over a seasonal timescale, which, despite the vast amount of prior research on this organism, was not previously known.

Materials and methods

Study system

Musk thistle, *Carduus nutans*, is an exotic invasive weed that is native to Europe and Asia and was first recorded in the USA near Harrisburg, PA, in 1853 (Desrochers *et al.*, 1988). Over time, this invasive weed has spread to most states in the U.S.A. (Allen & Shea, 2006); it is the second most commonly listed noxious weed in northern U.S.A. (Skinner *et al.*, 2000). *Carduus nutans* is a monocarpic perennial (Desrochers *et al.*, 1988) and is typically found in agricultural fields, roadsides, pastures, disturbed areas, lawns and open fields. It causes considerable economic damage, as its unpalatable, prickly leaves repel most large grazers and thus reduce pasture productivity (Desrochers *et al.*, 1988).

Rhinocyllus conicus is a commonly used biocontrol agent of musk thistle, first released into the U.S.A. in 1969 (Kok & Surles, 1975; Rees, 1977). It established well, and is considered to be generally successful as a biocontrol agent in North America (Crawley, 1989). It is a univoltine weevil that oviposits on the bracts of the thistle flower heads. Larvae develop in the receptacle tissue where seeds normally form, and thus prevent seed production (Zwölfer & Harris, 1984; Kok, 2001).

Despite the widespread use of *R. conicus* for biological control of *C. nutans*, its movement abilities and how it distributes itself in response to this resource are not well understood. Larvae of *R. conicus* are relatively immobile; they grow and pupate within the flower head on which they have been oviposited (Zwölfer & Harris, 1984). Only the adult stage of *R. conicus* is mobile (the rest of the life cycle is completed within the thistle flower heads), and therefore here we have focused on the dispersal behaviour of the adults.

Experimental design

The study was carried out at the Russell E. Larson Research Center at Rock Springs, PA. The study site was a permanent hayfield with a predominant mixture of grasses and exotic weeds surrounded by cornfields, typical of the landscape of Pennsylvania. The field site was dominated by oatgrass (*Arrhenatherum elatius*), orchardgrass (*Dactylis glomerata*), Canada goldenrod (*Solidago canadensis*) and wild onion (*Allium* spp.); other vegetation included common milkweed (*Asclepias syriaca*), common dandelion (*Taraxacum officinale*), English plantain (*Plantago lanceolata*) and burdock (*Arctium* spp.). All exotic weeds in the family Cardueae (Canada thistle, *Cirsium arvense*, bull thistle, *Cirsium vulgare* and plumeless thistle, *Carduus acanthoides*) at or near the field site (within a 1 km range) were removed and the area was managed intensively throughout the course of the study. *Carduus nutans* does not grow wild at the Russell E. Larson Research Center. *Carduus nutans* seeds were collected from a naturalised population near Carlisle, PA, grown to rosette stage in the greenhouse, and then transplanted into the field for this study.

Carduus nutans plants were planted in patches of different area and number of plants; hence patch density also varied. The experimental design consisted of combinations of three patch areas (1, 4, 16 m^2) and three plant densities (1, 2, 4 thistles m^{-2}) and was replicated in five blocks (Figure S1). There were more (additional three per block in two of the blocks) planned replicates of the small patch area and low plant density treatment as we expected higher variation in these plots (some of these plots were indeed lost in the first year of the study). Conversely, there were only three replicates of the largest, high-density treatment, as we were constrained in the number of plants we could grow. Other measures of patch quality, such as plant height, number of stems per plant and number of flower heads per plant, were recorded as covariates. Patches were separated by 4 m on each side, which is the edge length for the largest patch area (Figure S1). Blocks were separated by a minimum distance of 46 m; their locations in the field were selected to maximise inter-block distances. The study was initiated in 2004 and repeated in 2005 with re-randomisation of the blocks and of the patches within the blocks.

Individually mark–mass release–resight

Weevils were field-collected from *C. nutans* plants from the same source population as the seed heads. Many were collected as mating pairs, and all were stored together until release; thus we assume weevils were highly likely to have mated before release. A broad range of techniques have been used to mark insects, the most common of which include body tags, mutilations, paints and inks, and dusts (Hagler & Jackson, 2001). Three criteria should be considered when selecting an appropriate marking technique: permanence, effects on individual, and whether marks are individual or mass (identical). Dusting techniques work well on hairy individuals, but cannot be individualised. Body tags are usually impractical because they affect movement of most small insects (Hagler & Jackson, 2001). Body mutilations done properly will not affect movement or survival in some species, and can be individualised (Johnson, 2004), but are challenging to apply to small insects. Non-toxic paints and dyes, such as color waterproof enamels, can be applied individually and are commonly used to mark insects (Opp & Prokopy, 1987), and particularly beetles (Harman, 1975; Humphry & Linit, 1989; McIntosh *et al.*, 1996). These marks are generally durable and, if applied correctly, have little effect on the beetle behaviour (Hagler & Jackson, 2001). For these reasons, Testor's Acrylic Paint (Vernon Hills, Illinois) was used to individually mark 1078 weevils in each year with up to two coloured spots on each of the two elytra; observations suggest that marking has no effect on weevil behaviour. Ninety-eight weevils were released at each of 11 release points at the end of May in a novel IMMRR design. One release was made within each of the five blocks, one release in the middle of the study area, and five releases outside the study area [one release to the south at 120 m (2004 only), four releases to the southwest of the field at 180, 460, 700 and 940 m (both years) and one release to the Southwest at 1250 m (2005 only)]. The maximum distance was motivated by the anecdotal records of *R. conicus* long-distance movement in Virginia and Georgia (Kok & Surles, 1975; Buntin *et al.*, 1993). The need for information on both long- and short-distance movement to explain distribution patterns motivated the release of insects both within the study area and at a range of distances away from the study area, and the integration of MMR and IMRR methods. The 1:1 sex ratio observed in naturally occurring populations (Z. Sezen, pers. obs.) was maintained at each release point (approximately in 2004, and exactly in 2005, when each individual was sexed prior to release). Resident weevils were removed from the field site prior to release of the marked weevils to ensure that the density of weevils remained within the natural range after the mass release. A total of 995 weevils were removed from the field site in 2004; there was no natural colonisation in the second year prior to our releases.

Immediately following release, resight censuses were carried out three times a day to capture the initial patch location by the majority of the weevils. After the first few days, resight censuses were carried out every 2 or 3 days (2004) or every weekday (2005) until weevil activity had ceased (the end of June in both years), except on days with heavy rain (as most insects avoid movement during bad weather (Kareiva, 1982)). Simultaneous censuses, during which each individual thistle was carefully inspected for marked weevils, were carried out in each of the five blocks.

Data analyses

A number of statistical and mechanistic methods have been utilised to understand the patterns, causal factors, and underlying mechanisms of insect movement in spatially heterogeneous environments (Vinatier *et al.*, 2011). We utilised a combination of statistical and mechanistic model approaches, each addressing different components of our overall question about insect movement. First, we studied initial patch location by weevils, using first weevil encounter records. Second, we used the program MARK (White & Burnham, 1999) to model within-season weevil apparent survival (defined as surviving and remaining in the study area) and sighting probability within the study area (Johnson, 2003). Third, we used a spatial model to assess how weevil movement between the patches is affected by the characteristics of the host-plant patch. The latter two analyses were performed on the complete encounter histories of the individual weevils.

Weevil responses to patch area and plant density were examined based on the first encounter of each weevil. As the first resight surveys were conducted 2 and 4 h after the release, and the majority of the weevils were encountered within the first few days of the release in both years of the study (Figure S2), we assume that weevils were first observed in the patch they located first. Distance to the nearest release point and patch level covariates, such as average and maximum height of plants in each patch, total number of flower heads in a patch and average number of flower heads in a patch, were also tested. We fit generalised linear mixed-effects regression models using penalised quasi-likelihoods in R (R Development Core Team, 2006) to determine the effect of our treatments and patch level covariates on the number of weevils resighted per patch and per plant averages at the patch level. We included patch area and plant density as fixed effects, and block and year as random effects.

The models were fit with a quasi-Poisson distribution (with a log link function) to account for overdispersion in the data, and the best fits were chosen by comparing Akaike information criterion (AIC) values (Burnham & Anderson, 2002).

We used MARK to model apparent survival and detection probability, and test hypotheses relating to survival for each year of the 2 years of mark–release–resight study. MARK is a simulation program that was developed for the analysis of mark–recapture data and is widely used to obtain survival and population estimates from encounter histories of marked animals (Johnson, 2004; Zimmermann *et al.*, 2011; Chiari *et al.*, 2014; Dolny *et al.*, 2014; Niemela *et al.*, 2015). We used the Cormack–Jolly–Seber (CJS) model to estimate survival (φ) and recapture rates (ρ) of *R. conicus*. MARK estimates model parameters using maximum likelihood techniques and ranks competing models in the order of best fit, which is determined by the lowest AIC; the approach is described in detail by Lebreton *et al.* (1992). Each competing model makes different assumptions about the dependence of weevil survival and capture probability on time and sex of the weevils. Analyses were performed separately for the censuses that were carried out in 2004 and 2005, which consisted of 17 and 26 sample periods, respectively. Time dependence in survival and recapture was tested for both years, but the effect of sex could only be included as a factor in the second year (2005).

Due to the limitations of the multi-strata model (maximum of 26 patches allowed) in MARK, we used a movement model (Johnson, 2003) in MATLAB (Mathworks, Natick, MA, USA, 2012) to test the dependence of weevil movement on the number of thistles in a patch (patch size). We selected patch size instead of patch density because the movement model AIC analysis identified the patch size models as the better fits (see Results). We estimated the following four parameters using a stochastic estimation method, simulated annealing: (i) η, probability of dispersing out of the smallest patch (one plant) over one time step; (ii) α, decay of dispersal probability with distance; (iii) ζ_{e}, patch size-dependent emigration; and (iv) ζ_{i}, patch size-dependent immigration. Simulated annealing is an iterative process to search the multi-dimensional parameter space to find the parameter value set with the global maximum likelihood given the data sets of movement and non-movement events (Kirkpatrick *et al.*, 1983). A distance matrix was created from the spatial coordinates of patches. In the iterative process, we changed each parameter value independently by sampling the displacement value and direction from a mean of zero and a normal distribution. Each model was fitted using 30 000 iterations. For each iteration, the probabilities of leaving patch sizes N_i, probabilities of entering patch sizes N_j, and the probabilities of moving the distance between patches i and j, where $i \neq j$, were calculated. In the full model, the probability of leaving patch i after one time step is a function of the number of plants in the patch (N_i) and is equal to

$$\eta N_i^{\zeta_{\mathrm{e}}};$$

thus, the probability of remaining in patch i after one time step is

$$p_{i,i} = 1 - \eta N_i^{\zeta_{\mathrm{e}}}.$$

The relative probability of moving from patch i to patch j, conditional on leaving patch i, is a function of the distance between patches i and j multiplied by the probability of entering a patch the size of patch j,

$$p'_{i,j} = N_j^{\zeta_{\mathrm{e}}} \mathrm{e}^{d_{i,j}\alpha}.$$

This relative probability was rescaled such that movement from patch i to all patches k, where $k \neq i$ but includes j, equals the probability of emigrating from patch i, such that:

$$p_{i,j} = \frac{\left(p'_{i,j}\right)}{\sum_k p'_{i,k}} * \eta N_i^{\zeta_{\mathrm{e}}}.$$

All $p_{i,j}$ values were inserted into a probability matrix (**M**) that characterises movement probabilities throughout the experiment over 1 day. When the time interval (I) between observations was greater than 1 day, the probability matrix was raised to the power of the number of days, $\mathbf{M_I} = \mathbf{M^I}$. Eight models were tested for each year of data: the full model where all four parameters were estimated and seven reduced models where one or more of the parameters were constrained. We did not test the null model with $\eta = 0$, which would mean that there was no dispersal; we know that dispersal occurred. The eight models for each year were compared using AIC values where models with $\Delta\mathrm{AIC} < 3$ were acceptable. Confidence intervals (CIs) of parameter estimates were calculated by bootstrapping (sampling with replacement) the weevil movement data. Additionally, the models were assessed using two different dispersal functions (power decay and exponential decay).

Results

Approximately twice as many weevils were resighted at least once in the first year of the study than in the second (Table 1): 27% and 13% in 2004 and 2005, respectively. There were also approximately twice as many encounters in the first year as the second (Table 1), despite the higher number of censuses (17 vs. 26, respectively) in the second year of the study. None of the weevils that were released at the furthest release point in 2005, at 1250 m, were resighted, but in both years weevils that were released from the release point at 940 m from the center of the field were resighted (Table 1). In both years of the study, approximately a third of all resighted weevils were sighted only once (106 in 2004 and 54 in 2005); the maximum number of times a weevil was resighted was 12 in the first year and 14 in the second year. The proportion of weevils resighted decreased with distance of the release point to the field site (Fig. 1). In 2005, the numbers of marked females (71) and males (69) encountered throughout the sampling period were not significantly different ($\chi^2 = 0.03$, df = 1, $P > 0.05$).

Weevil response to patch area and plant density

Patch area, average plant height per patch, and the distance to the nearest release point were the most significant predictors

Table 1. Summary of weevil resights and longest distances recorded for the 2 years of the individually mark–mass release–resight study.

Year	2004	2005
Number of weevils released	1078	1078
Number of weevils resighted	286	140
Percent of weevils resighted (%)	27	13
Number of encounters	939	453
Longest recorded initial movement (m)	909	852

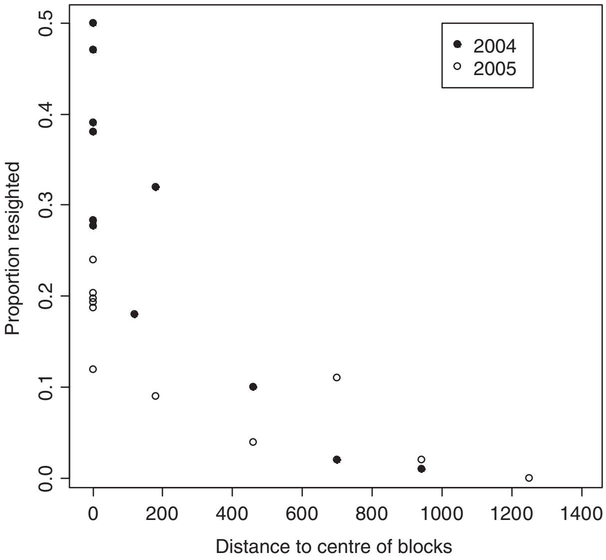

Fig. 1. Proportion of weevils resighted from each release point as a function of the distance to the centre of the blocks.

of the number of weevils resighted within a patch (Table 2a). More weevils were first observed in larger patches than in small and medium patches, and more weevils were subsequently observed in medium- and high-density patches than in low-density patches. The patch area and plant density interaction was not found to be significant so it was dropped from the models.

When corrected for the number of weevils observed per plant for each patch, there was no effect of patch area or plant density on the number of weevils resighted (Table 2b). The average height of plants in a patch and the distance to the nearest release point were both highly significant predictors of the number of weevils resighted per plant ($P \leq 0.001$). The negative effect of the distance to the nearest release point was almost 10 times the positive effect of the average plant height for a patch. In summary, weevils found taller and closer thistle patches first. We did not find an effect of sex on first weevil resights across patch types.

MARK *and the migration model*

A number of models were constructed in MARK to test time dependence in survival (φ) and recapture rates (ρ) for both years (Table S1). With the 2005 data, we were also able to test whether there was a difference in these rates between the two sexes. In 2004, time dependence in both apparent survival and recapture rates was supported by the best-fit model (Table 3). In 2005, apparent survival was found to be time-dependent for the three most parsimonious models but there was no effect of sex on survival (Table 3). As $\Delta\text{AIC} < 2$ for the two models, $\varphi_t\rho$ and $\varphi_t\rho_s$, both models (given time dependence in survival rates, sex dependence and no sex dependence in recapture rates) have approximately equal weight in the data. The model with time-dependent recapture rates had very little support for 2005 (Table 3). In the models that fitted the data best for both years apparent survival rates differed temporally within a season. In both years, apparent survival rates per survey were depressed in the initial sampling period (82% ± 8% and 62% ± 17% in 2004 and 2005, respectively). Apparent survival rates then increased to 96% and higher in 2004, and 92% and higher in 2005 in the subsequent sampling periods. Recapture rates generally decreased with time in 2004, from ranges of 17–59% in the first 13-sample period to 1–5% in the last three-sample periods. In 2005, the best-fit models had constant recapture rates of 46% ± 2% for all weevils, or 44% ± 3% for males and 47% ± 3% for females measured separately (Table S2).

Our migration model results were similar for both exponential decay (Table 4) and power decay (results not shown) dispersal functions. The full model fitted the 2004 movement data best (based on all $\Delta\text{AIC} > 28$) (Table 4). The full model also fitted the 2005 movement data best, but when we used an exponential decay function, there also was strong support ($\Delta\text{AIC} = 0.4$) for the data with no patch size-dependent emigration (ζ_e). In 2004, the probability per day of moving out of a patch with a single plant was estimated at $\eta = 0.07$. This probability of moving decreased ($\zeta_e = -0.86$) as patch size increased, meaning that weevils were more likely to disperse out of a small patch than out of a large patch (Table 5). For example, a weevil was 83% less likely to disperse from a patch with eight thistles than a patch with one thistle. In 2005, the probability per day of moving out of a patch with a single plant was less, an estimated ($\eta = 0.025$), but there was no evidence of patch size-dependent emigration because the 95% CI crossed zero in the full model, and patch size-dependent emigration was not included in the reduced model (Table 5). In both years, the patch size-dependent immigration parameter was significantly greater than zero and similar in magnitude (Table 5; $\zeta_i = 1.16$ in 2004, $\zeta_i = 1.14$ in the 2005 full model, and $\zeta_i = 1.06$ in the 2005 reduced model), meaning that weevils were 11.15, 10.70 and 9.06 times more likely to disperse into a patch with eight thistles than a patch with one thistle. When these numbers are converted to a per-plant basis, the probability of moving to a thistle in a patch with eight plants is 13–39% greater than moving to the single thistle in a patch size of one. All best fit models included α. The estimated values of α from the full models predict that the probability of movement to a patch decays by 50% for every 42 m distance in the 2004 data and for every 21 m distance in the 2005 data. However, the 95% CI for the 2005 data included zero in both the full and reduced models (Table 5), implying that spatial structure at the scale of the 2005 experiment may not have been important to weevil movement.

Table 2. Number of first resights (a) per patch and (b) per plant for each patch: generalised linear mixed-effects model results.

Fixed effects	Estimate	Standard error	t value	*P*-value	
(a) Number of first resights per patch					
(Intercept)	−0.168	0.516	−0.325	0.746	ns
Patch area	0.118	0.014	8.604	≤0.001	**
Plant density	0.202	0.081	2.489	0.015	*
Average plant height in patch	0.013	0.004	3.546	0.001	**
Distance to nearest release point	−0.134	0.027	−4.975	≤0.001	**
Fixed effects	**Estimate**	**Standard error**	**t value**	***P*-value**	
(b) Number of first resights per plant for each patch					
(Intercept)	−0.807	0.582	−1.387	0.169	ns
Patch area	−0.040	0.022	−1.827	0.071	ns
Plant density	−0.142	0.118	−1.206	0.231	ns
Average plant height in patch	0.017	0.004	3.867	≤0.001	**
Distance to nearest release point	−0.126	0.035	−3.646	0.001	**

*$P \leq 0.05$; **$P \leq 0.001$.

Results in (a) are based on total number of weevils first resighted within a patch and are not corrected for the number of plants within a patch. More weevils are resighted where there are more thistles present. ns, non-significant.

Table 3. Results for the most parsimonious models in MARK.

Model	AICc	ΔAICc	AICc weight	Model likelihood	#Par	Deviance
2004						
$\varphi_t\rho_t$	2277.031	0.00	0.99946	1.0000	31	889.598
$\varphi\rho_t$	2292.266	15.23	0.00049	0.0005	17	934.587
$\varphi_t\rho$	2297.030	20.00	0.00005	0.0001	17	939.351
2005						
$\varphi_t\rho$	1195.165	0.00	0.72615	1.0000	26	714.171
$\varphi_t\rho_s$	1197.123	1.96	0.27271	0.3756	27	713.838
$\varphi_t\rho_t$	1208.067	12.90	0.00115	0.0016	48	673.735

φ, apparent survival parameter; ρ, recapture parameter. Summary of the models that best support the data are given, from the full set of models tested in MARK (Table S1). Data from the 2 years of the study (2004 and 2005) were tested separately. For 2004, φ_t ρ_t, fully time dependent CJS model; $\varphi\rho_t$, resights are time-dependent and survival is constant; $\varphi_t\rho$, survival is time-dependent and resights are constant. For 2005, $\varphi_t\rho$, survival is time dependent and resights are constant; $\varphi_t\rho_s$, survival is time-dependent and resights are sex-dependent; $\varphi_t\rho_t$, fully time-dependent CJS model. AICc, corrected Akaike's information criterion.

Table 4. Parameters used in the migration models with an exponential decay dispersal function and Akaike information criterion (AIC) values of the models.

2004			2005		
Model	AIC	ΔAIC	Model	AIC	ΔAIC
$\eta, \alpha, \zeta_i, \zeta_e$	788.3	0	$\eta, \alpha, \zeta_i, \zeta_e$	542.7	0
$\eta, \zeta_e, \zeta_{i,}$	816.4	28.1	$\eta, \alpha, \zeta_{i,}$	543.1	0.4
$\eta, \alpha, \zeta_{i,}$	837.1	48.8	η, ζ_i	566.1	23.4
η, α, ζ_e	847.0	58.7	η, ζ_e, ζ_i	566.3	23.6
η, ζ_i	865.5	77.2	η, α	572.0	29.3
η, ζ_e	873.4	85.1	η, α, ζ_e	573.9	31.2
η, α	878.1	89.8	η, ζ_e	601.1	58.4
η	905.7	117.4	H	601.3	58.6

The best-fit models are shaded in grey. ΔAIC, difference between AIC for that model and AIC of the 'best' model (minAIC).

Discussion

Habitat patch size and isolation have been found to be two of the most important factors affecting dispersal and distribution of organisms (MacArthur & Wilson, 1963; Root, 1973; Kareiva, 1985; Matter, 1996 and references therein; Boeg & Eckert, 2013), although the resulting distribution may also be dependent on the dispersal behaviour of the particular organism and the cues it uses to locate its host (Bowman *et al.*, 2002; Bukovinszky *et al.*, 2005; Hambäck & Englund, 2005; Andersson *et al.*, 2013). Dispersal studies in general have focused on the effect of different distributional outcomes but have often failed to describe the underlying movement behaviour that generates the observed patterns (Kareiva, 1982; Hambäck *et al.*, 2014). Studies that ignore factors affecting host plant location by the herbivore give an incomplete picture of the causal mechanisms of resulting herbivore distributions.

Prior to this study, there was relatively little information on the dispersal abilities of *R. conicus*, and dispersal of these weevils was thought to be minimal, especially after initial release (Kok & Surles, 1975). Our study has shown that *R. conicus* is very mobile and is able to rapidly locate thistle host plant patches from nearly a kilometre away within a few days. There is also an indication that weevils preferentially moved towards the thistles (significantly more weevils were resighted on the

Table 5. Parameter estimates for the best-fit model for the 2004 movement data, and for the top two models for the 2005 movement data.

	η	α	ζ_e	ζ_i
2004				
Full model	0.070 [0.044, 0.110]	0.016 [0.011, 0.026]	−0.86 [−1.13, −0.62]	1.16 [0.88, 1.68]
2005				
Full model	0.025 [0.011, 0.045]	0.033 [0.00, 0.26]	−0.23 [−0.62, 0.08]	1.14 [0.62, 1.71]
Reduced model	0.016 [0.011, 0.021]	0.033 [0.00, 0.23]	–	1.06 [0.68, 1.94]

A negative ζ_e value indicates that weevils are more likely to disperse out of small patches, and a positive ζ_i value indicates that the weevils are more likely to disperse into large patches. Numbers in square brackets are the 95% confidence limits of the parameter estimates. η, probability of dispersing out of the smallest patch ($1\,m^2$) over one time step; α, decay of dispersal probability with distance; ζ_i, patch size-dependent immigration; ζ_e, patch size-dependent emigration.

thistle patches than would be expected on the assumption that weevils move equally in all directions from their release point; χ^2 test, $P \leq 0.001$, in both years; Table S3), although further study would be necessary to completely eliminate potential confounding factors such as prevailing winds and non-linear dispersal patterns that we could not directly address in this study. The structure of the matrix (non-habitat) has also been shown to affect the movement of a broad range of taxa (Banks, 1998; Eycott *et al.*, 2012); again this is beyond the scope of our study.

We found that the number of weevils initially resighted increased with the height of plants within a patch and with proximity to release point. While the number of initial resights of weevils per patch increased significantly with plant density and highly significantly with patch area, there was no effect of patch area and plant density on the number of weevils resighted per plant in a patch. Additionally, weevils were more likely to disperse out of small patches and they were more likely to disperse into large patches. Our results broadly agree with hypotheses that organisms are commonly distributed in their environment in response to the distribution of resources or natural enemies in their environment (e.g. Fretwell & Lucas, 1970, 1972; Root, 1973; Hambäck *et al.*, 2014). Herbivores, for example, may aggregate in large and high-density patches of host plants (Kareiva, 1985; Grez & Gonzalez, 1995; Shea *et al.*, 2000), although results may depend on the relative spatial scale of movement and resource distribution in the landscape (Hambäck & Englund, 2005) and on whether olfactory or visual cues, or both, are used to locate hosts (Bukovinszky *et al.*, 2005; Hambäck & Englund, 2005; Andersson *et al.*, 2013). We expected immigration rates and residence time in a patch to increase with increasing resource availability, which we defined at the patch level as patch size (patch area × plant density) (Matter, 1997). With our migration model we found that, in this system, immigration rates and residence time did increase with patch size, as expected. Our results are in agreement with results obtained by Kareiva (1985) for flea beetles on collard patches, where he found that small patches were both easy to lose and hard to find. This leads to potential natural enemy escape opportunities for smaller host patches, as in the case of a single thistle plant not being located (found) by any weevils.

We did not find apparent survivorship to vary between the sexes, but the model with sex dependence in recapture rates in 2005 in MARK had good support. The recapture estimates were slightly higher for females than for males. Other studies have found that male insect herbivores are more mobile than females and more likely to leave a patch (Matter, 1996). If *R. conicus* males are spending more time between patches than in patches, then this could explain our result. The discrepancy in time dependence in the recapture rates for the 2 years may be attributable to phenology. The field season in 2005 was delayed and much shorter than usual, with less weevil activity overall and lower survival in the naturalised populations (Z. Sezen, pers. obs.). The depressed apparent survival in the early season in both years could be due to post-release dispersal, as survival probability (φ) is the combination of the proportion of weevils remaining in the entire study area and surviving. Some weevils are likely to have dispersed out of the study area at initial release, after which most weevils survived and remained within the study area throughout the sampling period. The high levels of apparent survival sustained throughout the sampling period in both years of the study indicate that most weevils remain within the study site and do not disperse in search of other host patches.

Understanding the movement behaviour and host location ability of herbivores is a fundamental requirement for a deeper understanding of coupled plant–herbivore dynamics on a landscape. For this reason, the integrative IMMRR approach we use here has great potential as a tool to enhance spatiotemporal ecological research. Understanding the movement behaviour of herbivores is also particularly important in applied systems, for example in biological control. Classical biocontrol agent testing has historically focused on feeding relationships, and has often neglected spatial aspects of the species' interactions. Ignoring spatial aspects may lead to mis-estimation of the ability of a biocontrol agent to regulate the population dynamics of its host in the field (Louda *et al.*, 2005). For example, recent work shows that *R. conicus* may have unrecognised spatial impacts, by reducing seed release and dispersal, in addition to its well-documented negative effects on seed production (Marchetto *et al.*, 2014). We focused on movement behaviour of biocontrol agents in response to their host plant patches in the introduced habitat, which is critical to assessing and improving biological control efforts (Louda *et al.*, 1997, 2003a,2003b; Louda, 2000; Arnett & Louda, 2002); failing to do so imposes limits on our abilities to predict the effectiveness of potential biocontrol agents. For example, the spacing of initial releases of biocontrol agents should be scaled by the agents' movement ability; releases made too close together will congregate insects that could more effectively be widely dispersed, while releases made too far apart may lead to long times until gaps between releases are colonised, delaying control on the landscape. Here we have shown that, even though *R. conicus* quickly travels far greater distances immediately after initial release than previously recorded, it may fail to locate, or leave undetected from small, isolated, plant patches of the invasive thistle, *C. nutans*, when it is distributed heterogeneously in space. This is predicted, in turn, to have significant impacts on the ecology of this interaction at larger scales (Sezen, 2007), where the spread of the invasive thistle may be driven by smaller patches that have escaped attack. Information on how a biocontrol agent detects its host and how far it is able to disperse on its own, combined with information on host species distribution in the landscape, will critically aid management efforts to control spatial spread of invasive species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12383

Figure S1. Spatial arrangement of the experimental patches in the field.

Figure S2. Number of first encounters of weevils by number of days after release in both years of the study.

Table S1. Summary of models constructed in program MARK.

Table S2. Apparent survival and recapture probability estimates from the most parsimonious models in program MARK.

Table S3. χ^2 test for attraction to thistle field.

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