Dispersion of a carabid beetle in farmland is driven by habitat-specific motility and preference at habitat interfaces

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Abstract

Carabid beetles are common predators of pest insects and weed seeds in agricultural systems. Understanding their dispersal across farmland is important for designing farms and landscapes that support pest and weed biological control. Little is known, however, about the effect of farmland habitat discontinuities on dispersal behaviour and the resulting redistribution of these beetles. We released 1,985 well-fed and 1,680 food-deprived individuals of the predatory carabid beetle Pterostichus melanarius (Illiger) (Coleoptera: Carabidae) on a farm in Wageningen, The Netherlands. We recaptured 23.6% of those beetles over a period of 23 days in 2010. The farmland comprised agricultural fields with various crop species and tillage, separated by strips of perennial vegetation. We developed discrete Fokker-Planck diffusion models to describe dispersal based on motility ($m^2 \cdot d^{-1}$) and preferential behaviour at habitat interfaces. We used model selection and Akaike’s information criterion to determine whether movement patterns were driven by variation in motility between habitats, preferential behaviour at habitat interfaces, or both. Model selection revealed differences in motility among habitats and gave strong support for preferential behaviour at habitat interfaces. Behaviour at interfaces between crop and perennial vegetation was asymmetric, with beetles preferentially moving towards the crop. Furthermore, beetles had lower motility in perennial strips than in arable fields. Also between arable habitats movement was asymmetric, with beetles preferentially moving towards the habitat in which motility was lowest. Neither crop type nor tillage explained differences in motility between crop habitats. Recapture data representing dispersal patterns of beetles were best described by a model that accounted for differences in motility between farmland habitats and preferential behaviour at habitat interfaces. Motility in farmland and behaviour at interfaces can also be estimated for other organisms and farmland habitats to support design of farmland conducive to natural pest suppression. Landscape design for early recruitment of carabids into arable fields should take into account the quantity and quality of resource habitats in the landscape, their proximity to crop fields, movement rates, and the possibility of movement responses at interfaces between landscape elements.

Introduction

Since the 1980s of the 20th century, agricultural landscapes have undergone progressive homogenization, resulting in biodiversity decline (Foley et al., 2005). There is currently

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great interest in halting this biodiversity loss or even trying to increase biodiversity by landscape redesign for enhanced delivery of ecosystem services, such as biological pest suppression and pollination. The redesign of farmland for pest suppression requires practical guidelines for the types, sizes, and patterns of farmland habitats and their connectedness by dispersal (Steingrüber et al., 2010). Strengthening the scientific basis of these guidelines is important to enhance cost-effectiveness of habitat manipulations and to support and motivate land managers.

*Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae) is a common predatory beetle in agricultural land (Thiele, 1977). It feeds on a broad range of epigeal invertebrates and contributes to biological pest control (Sunderland, 2002). Here we measured within-season dispersal of *P. melanarius* to determine how differences in movement between farmland habitats and preference behaviour at habitat interfaces affect dispersal of released beetles.

Movement is defined as a change in the spatial location of an individual, whereas dispersal is defined as the continuous change in the spatial pattern of occurrence of populations or population redistribution (Schellhorn et al., 2014). Population redistribution in a homogeneous habitat can be modelled using Fokker-Planck diffusion (Turchin, 1998; Ovaskainen, 2008), whereas behavioural responses to habitat interfaces can be modelled using preference indices (Cantrell & Cosner, 1999; Ovaskainen & Cornell, 2003; Maciel & Lutscher, 2013). The parameter representing the rate of population spread in a Fokker-Planck modelling framework is denoted as motility with unit m² day⁻¹ (Turchin, 1998; Allema et al., 2015). Motility in the Fokker-Planck equation is similar to diffusivity in the Fickian diffusion model, but whereas diffusion events out differences in density between adjacent habitats, even if the diffusivity is spatially heterogeneous, the same is not the case for a Fokker-Planck model (Turchin, 1998). When a given population redistributes over space and habitat interfaces do not influence behaviour, the relative difference in density between two habitats is, at equilibrium, proportional to the inverse of motility within these habitats (Turchin, 1998; Allema et al., 2014). This is different from ordinary diffusion in which density events out completely, even if the diffusion coefficient differs between the habitats. When a species has a preference for one or the other habitat when it is at their interface, e.g., due to olfactory cues acting over a short distance, this can lead to a steep change in density at the habitat interface, even if motility within the habitats is equal (Haynes & Cronin, 2003; Ovaskainen & Cornell, 2003). Little is known about the importance of differences in motility and the effects of behavioural responses at interfaces on the distribution of biota in farmland.

Although a detailed discussion on modelling interface behaviour in patchy landscapes is emerging (Maciel & Lutscher, 2013; Musgrave & Lutscher, 2014), few empirical ecologists have parameterized spatial models that include interface behaviour on ecological data (Ovaskainen et al., 2008a,b) or agricultural systems (Bommarco & Fagan, 2002). In this paper, we address the question how farmland habitats and their spatial structure affect the redistribution of *P. melanarius* over the course of a crop growing season. Answering this question will, to our knowledge for the first time, show the role of different farmland habitats, i.e., crops and semi-natural elements in population pattern formation for an important pest predator, providing quantitative information to design farmland for pest suppression. To answer the question, we implemented a Fokker-Planck model in discrete time and added to it preferential behaviour at habitat interfaces using flux-modifiers. Other studies have used continuous time diffusion approaches instead (e.g., Ovaskainen & Cornell, 2003; Maciel & Lutscher, 2013). We chose here a discrete time approach because it is computationally efficient. We hypothesize that population patterns are the result of differences in motility between farmland habitats and of preferential behaviour at habitat interfaces.

### Methods

#### Experimental farmland and habitats

A mark-recapture study was conducted in the summer of 2010 at the organic experimental farm Droevendaal (51°5′N, 05°40′E, 20 m a.s.l., Wageningen, The Netherlands). The farm was situated on sandy soil with about 3% organic matter. The experiment was laid out on 175 × 250 m of farmland (4.375 ha), comprising five crop fields and two perennial strips (Figure 1). In fields 1–4 spring barley (*Hordeum vulgare* L. cv. Quench, Poaceae) was grown and in field 5 yellow mustard (*Sinapis alba* L. cv. Achilles, Brassicaceae). Fields 1 and 2 were left unploughed, thereby reducing disturbance and preserving soil fauna, whereas fields 3–5 had been conventionally ploughed on 16 April. Margin 1 (Figure 1) was 7 m wide and consisted of tall grasses, herbs, and a 6-year-old hedge-row. Margin 2 was 6.5 m wide and consisted of a 4-m-wide strip with a mixed vegetation of grasses and herbs as in margin 1, but without a hedgerow, and a 2.5-m-wide strip with grass/clover immediately adjacent to it. To avoid confusion later in this paper we now add how these seven different parts of the considered farmland habitat are numbered in the models: (1) field 1, (2) margin 1, (3) field 2, (4) field 3, (5) margin 2, (6) field 4, and (7) field 5.

Adult *P. melanarius* for release in the mark-recapture study were collected from pitfall traps in fields 2 and 3 at
Beetles were stored in containers (45 \times 30 \times 15 \text{ cm}; 400 beetles per container) on a substrate of moist potting soil in a dark room at 12 °C. During storage, beetles were fed defrosted dipteran larvae [*Lucilia caesar* (L.), Calliphoridae]. Two groups of beetles were prepared for release: food-deprived and well-fed beetles that will be referred to as starved and non-starved beetles. These two groups were included because feeding condition has been found to affect movement in carabids (e.g., Mols, 1993). The non-starved beetles received 22 mg of maggots per beetle twice a week, i.e., 132 mg per beetle over 3 weeks. The starved beetles were fed one-sixth of this amount. On 21 July, the average (\pm SE) body weights of starved and non-starved beetles were 0.141 ± 0.004 and 0.174 ± 0.004 g, respectively (two-sample t-test: \( t = 5.93, \text{ d.f.} = 58, P < 0.0001 \)). Only female beetles were used in the release because in a previous field study on carabid movement patterns no significant differences related to hunger level or prey density were found for male *P. melanarius* (Wallin & Ekbom, 1994).

Releases were made from release stations on three lines in the experimental farmland, at 55 m (line A), 131 m (line B), and 207 m (line C) from the northern short edge (Figure 1). Each line had five release stations, consisting of 37 \times 56 \times 7 \text{ cm} trays with holes at the soil surface to allow beetles to leave. The trays were placed in the field on 20 July at 19:00 hours. The number of non-starved and starved beetles released was 720 and 620, respectively, on line A, 680 and 465 on line B, and 585 and 595 on line C. The following morning, almost all beetles had left the trays and a few remaining individuals were shaken out gently. Before release, the beetles’ elytra had been marked with nail polish (OPI Nail lacquer) according to the beetle’s diet treatment (two levels) and release locations (three lines), resulting in six marker colours.

Recaptures were made using pitfall traps. Trapping stations were spaced 10 m apart in the north–south direction and 9–17 m apart in the east–west direction (Figure 1). At each trapping station, two pitfall traps were placed at 1 m distance from each other. The traps consisted of an inner and outer plastic cup (8.5 cm diameter) and a black plastic disk for rain cover. Recaptures made in the two traps per station were added before analysis. During the first 2 weeks after release, traps were emptied every day except on weekends. Thereafter, traps were emptied at time intervals of 2–6 days until 11 August. Sampling in field 1 was discontinued after 30 July when the crop was harvested.

The collected data comprised the number of beetles of each of the six marker colours recaptured at each trapping station and each sampling date.

**Analysis of mark-recapture data**

*Discrete Fokker-Planck model.* We implemented discrete Fokker-Planck models to estimate parameter values for the mark-recapture experiment. In the models, space was discretized into cells containing beetles that could move to adjacent cells (Figure 2) depending on cell-specific attributes (habitat, beetle density, or presence of a trap) and the habitat of the neighbouring cell, which could affect the beetles’ preference for moving there.
We used model selection (Burnham & Anderson, 2003; Bolker, 2008) to determine how the redistribution of *P. melanarius* under field conditions is driven by changes in motility between habitats and by preferential behaviour at edges. To this end, Fokker-Planck models representing different assumptions on the drivers were formulated and fitted to the data. The models considered diffusion in the x-direction ('1-D') only to reduce computation time during model calibration (typically exceeding 1 day of computation on the computer network used). We checked that this simplification did not affect conclusions by comparing results of the ultimately selected model with those of a 2-D variant.

To fit the 1-D models, we summed the data over the y-direction to calculate the number of released beetles at given x-location. Similarly, the data from the trapping stations on each x were summed (Figure 1). The 1-D model considering only movement in the x-direction was fitted to these beetle counts (Figure 2).

The general discrete time model can be written as (see also the Supporting Information):

\[
\Delta N_i(x,t) = N_i(x, t + \Delta t) - N_i(x, t) = I_{x,i} - (\xi_i + \alpha_i(x)) N_i(x, t) \cdot \Delta t, \tag{1}
\]

where \(N_i(x,t)\) (m\(^{-2}\)) is the density of starved \((i = s)\) and non-starved \((i = n)\) beetles at time \(t\) and location \(x\); \(\alpha_i(x)\) is the relative rate of beetle removal by a trap at location \(x\) (hereafter: relative capture rate, day\(^{-1}\)); and \(\xi_i\) is the relative loss rate of marked beetles due to death or mark wear (hereafter: relative loss rate, day\(^{-1}\)). \(I_{x,i}\) represents the net rate of change of beetle density in a grid cell at location \(x\) due to fluxes over the border with adjacent cells:

\[
I_{x,i} = \frac{\mu_i(x-1)N_i(x-1,t) - 2\mu_i(x)N_i(x,t) + \mu_i(x+1)N_i(x+1,t)}{\Delta x^2}, \tag{2}
\]

where \(\mu_i(x)\) denotes the motility of beetles (m\(^2\) day\(^{-1}\)) at location \(x\).

To account for greater trapping rates when movement increases, the relative capture rate \(\alpha_i(x)\) was assumed to be a linear function of \(\mu_i(x)\) according to:

\[
\alpha_i(x) = \begin{cases} 
\alpha_0 \mu_i(x) & \text{at trapping locations} \\
0 & \text{at other locations}
\end{cases}, \tag{3}
\]

where \(\alpha_0\) (m\(^{-2}\)) represents the trapping efficiency, which depends on trap properties and the propensity of beetles to fall into the trap given encounter with the trap. For each model we calibrated the parameters \(\alpha_0\) and \(\mu_i(x)\) to the field data and calculated \(\alpha_i(x)\) from these.

Models with different levels of complexity were formulated to account for the potential effect of differences in motility between the seven habitats (five fields and two margins) and for preferential behaviour at habitat interfaces (six interfaces for the seven habitats). Preferential behaviour at an interface was modelled by multiplying fluxes from one habitat to another by a factor, the so-called flux-modifier. Preferential behaviour occurs when the estimate for the flux-modifier from right to left \((p_{R \rightarrow L})\) is different from the estimate for left to right \((p_{L \rightarrow R})\) see.
Figure 2; Allema et al., 2014). Because the estimates of the two flux-modifiers are highly correlated, one of them (\(\pi_{9} \rightarrow l\)) was set to 1. We therefore estimated at each interface the value of only one flux-modifier \(\pi\), which represented the ratio \(\pi_{1} \rightarrow g/\pi_{9} \rightarrow l\). Preferential behaviour at the interface (i.e., values of \(\pi\) different from 1) will lead to step changes in the number of beetles in adjacent cells with different habitats. Differences in estimated motility at both sides of a border also result in such step changes (p. 84 in Turchin, 1998). However, differences in estimated motility at both sides of a border affect dispersal within these fields, whereas preferential behaviour at the interface only affects distribution between the fields; hence, calibration to data can help to identify the role of preferential behaviour at the interface.

The simplest model assumed that all beetles showed the same behaviour in each farmland habitat, i.e., a single motility value was estimated, preference at habitat interfaces was assumed absent, and the coefficients for trapping efficiency and a combined rate for loss of mark and death were independent of feeding level, resulting in a model with only three parameters. The most complex model included 30 parameters to be fitted to the data (see Table 1): 14 motilities for each of seven habitats and for non-starved as well as starved beetles (7 \(\times\) 2), 12 parameters for preference behaviour at habitat interfaces (six interfaces; non-starved and starved beetles), two parameters for loss rate (for non-starved and starved beetles), and two parameters for capture rate \(\alpha\) (for non-starved and starved beetles). The theoretical number of possible models is at least in the order of 2^30 (i.e., one billion) because each parameter could be included for non-starved and starved beetles separately, included as a single value for non-starved and starved beetles jointly, or excluded. With so many candidate models and a computationally intensive method for parameter identification (see below), it was impossible to explore all possible combinations of ecological hypotheses. A stepwise approach was therefore followed to search for the most satisfactory model containing the minimum number of ecological components needed to meaningfully describe the data. Model selection proceeded from the most complex model with 30 parameters to ever-simpler models until the Akaike information criterion (AIC), which was used as the criterion in model selection, could not be further reduced. We call the resulting minimum-AIC model the most satisfactory model. This model contains all those ecological components that make a meaningful contribution to the description of the data (Hilborn & Mangel, 1997; Bolker, 2008). Details of the fitted models are given in Appendix A. We used a time step for the integration of 0.001 day.

**Model selection.** During model selection, a suite of candidate models is fitted to data with maximum likelihood and an information criterion is used to compare the goodness of fit of the models, penalizing models that require many parameters to ‘explain’ the data (Hilborn & Mangel, 1997; Bolker, 2008). The AIC is

| Parameter | Description | Unit |
|-----------|-------------|------|
| \(\mu_1(x)\), \(\mu_{1,0}(x)\), \(\mu_{1,2}(x)\) | Motility of all, starved or non-starved, beetles in field 1 (barley no-tillage) \(x \in (0, 40)\) | \(m^2\text{ day}^{-1}\) |
| \(\mu_2(x)\), \(\mu_{2,0}(x)\), \(\mu_{2,2}(x)\) | Motility of all, starved or non-starved, beetles in margin 1 (grass strip plus hedgerow) \(x \in (40, 45)\) | \(m^2\text{ day}^{-1}\) |
| \(\mu_3(x)\), \(\mu_{3,0}(x)\), \(\mu_{3,2}(x)\) | Motility of all, starved or non-starved, beetles in field 2 (barley no-tillage) \(x \in (45, 88)\) | \(m^2\text{ day}^{-1}\) |
| \(\mu_4(x)\), \(\mu_{4,0}(x)\), \(\mu_{4,2}(x)\) | Motility of all, starved or non-starved, beetles in field 3 (barley conventional tillage) \(x \in (88, 140)\) | \(m^2\text{ day}^{-1}\) |
| \(\mu_5(x)\), \(\mu_{5,0}(x)\), \(\mu_{5,2}(x)\) | Motility of all, starved or non-starved, beetles in margin 2 (grass strip without hedgerow) \(x \in (140, 145)\) | \(m^2\text{ day}^{-1}\) |
| \(\mu_6(x)\), \(\mu_{6,0}(x)\), \(\mu_{6,2}(x)\) | Motility of all, starved or non-starved, beetles in field 4 (barley conventional tillage) \(x \in (145, 195)\) | \(m^2\text{ day}^{-1}\) |
| \(\mu_7(x)\), \(\mu_{7,0}(x)\), \(\mu_{7,2}(x)\) | Motility of all, starved or non-starved, beetles in field 5 (mustard) \(x \in (195, 250)\) | \(m^2\text{ day}^{-1}\) |
| \(\mu_8(x)\) | Motility in margin 1 and 2 \(x \in (40, 45)\) \(U\) (140, 145) | \(m^2\text{ day}^{-1}\) |
| \(\mu_9(x)\) | Motility in field 2 and 5 \(x \in (45, 88)\) \(U\) (195, 250) | \(m^2\text{ day}^{-1}\) |
| \(\mu_{10}(x)\) | Motility in field 1, 3, and 4 \(x \in (0, 40)\) \(U\) (88, 140) \(U\) (145, 195) | \(m^2\text{ day}^{-1}\) |
| \(\pi_{1,0}\), \(\pi_{2,0}\), \(\pi_{3,0}\) | Motility of all, starved or non-starved, beetles in the whole spatial domain \(x \in (0, 250)\) | \(m^2\text{ day}^{-1}\) |
| \(\pi_{1,1}\), \(\pi_{2,1}\), \(\pi_{3,1}\) | Flux-modifier for the flux of all, starved or non-starved, beetles from field 1 to margin 1 | – |
| \(\pi_{2,2}\), \(\pi_{3,2}\), \(\pi_{4,2}\) | Flux-modifier for the flux of all, starved or non-starved, beetles from margin 1 to field 2 | – |
| \(\pi_{3,3}\), \(\pi_{4,3}\), \(\pi_{5,3}\) | Flux-modifier for the flux of all, starved or non-starved, beetles from field 2 to field 3 | – |
| \(\pi_{4,4}\), \(\pi_{5,4}\), \(\pi_{6,4}\) | Flux-modifier for the flux of all, starved or non-starved, beetles from field 3 to margin 2 | – |
| \(\pi_{5,5}\), \(\pi_{6,5}\), \(\pi_{7,5}\) | Flux-modifier for the flux of all, starved or non-starved, beetles from margin 2 to field 4 | – |
| \(\pi_{6,6}\), \(\pi_{7,6}\), \(\pi_{8,6}\) | Flux-modifier for the flux of all, starved or non-starved, beetles from field 4 to field 5 | – |
| \(\xi\), \(\theta_0\), \(\theta_n\) | Global loss rate for mortality and mark wear for all, starved or non-starved, beetles | \(\text{day}^{-1}\) |
| \(\phi\), \(\psi\), \(\sigma\) | Global trapping efficiency for all, starved or non-starved, beetles | \(m^{-2}\) |
calculated as $\text{AIC} = 2 \cdot \mathcal{L} + 2 \cdot \text{Npar}$ in which $\mathcal{L}$ is the negative log likelihood (described below) and $\text{Npar}$ the number of parameters. Models are considered equivalent when their AIC values differ in value by two or less (Bolker, 2008). When the difference in AIC is larger than two, the addition or removal of a parameter contributed to model fit. Negative log likelihood was calculated for a given model as:

$$\mathcal{L} = - \sum_{t,x} \ln \left( L(Y_{t,x}|f(t,x,P)) \right),$$

where $L$ is the likelihood of the data $Y_{t,x}$ according to a negative binomial distribution, given model predictions $f(t,x,P)$ at trap location $x$ and time $t$, based on parameter vector $P (\in \mathbb{R}^{\text{Npar}})$. A negative binomial likelihood was chosen because of a high number of zeros in the catch data. This is generally known as zero-inflated data (see Zuur et al., 2009). In addition, the negative binomial distribution can represent discrete distributions ranging from a Poisson to a geometric distribution, depending on the parameter $k$ (Bolker, 2008). By optimizing $k$ we let the data ‘choose’ the distribution that would best describe the variability. The dispersion parameter $k$ of the negative binomial distribution was estimated once ($k = 1.45$) by calibration using model 8 (Table 2) and was then fixed during the calibration of the model variants. The negative log likelihood was minimized using a differential evolution algorithm (Storn & Price, 1997), implemented in reusable C++ code that is part of the COMPASS framework (Groot et al., 2012). This algorithm was chosen because of its power and versatility to find a global optimum (Das et al., 2016). The calibration was conducted using parallel computing in a network of 20 PCs.

**Workflow of model selection**

Model selection was broken up into four steps. The model with most support of the data in one step was used as the starting point (‘full model’) in the next step.

**Step 1.** In the first step, we evaluated whether it was relevant to account for feeding level of beetles. This evaluation was prioritized because feeding level might affect all parameters. We assessed the influence of feeding level on motility, loss rate, and trapping efficiency without accounting for habitat heterogeneity. The results showed that feeding level significantly affected the overall motility and loss rate of beetles. Therefore, in the subsequent analyses we calibrated loss rate, motility, and preference behaviour at edges separately for non-starved and starved beetles.

**Step 2.** In the second step, we investigated the influence of habitat heterogeneity and feeding level on movement behaviour. We tested three hypotheses: (1) distribution patterns are influenced by variation in motility between habitats, but not by preferential behaviour at habitat interfaces, (2) distribution patterns are influenced by preferential behaviour at habitat interfaces, but not by variation in motility, and (3) distribution patterns are influenced by both motility differences between habitats and preferential behaviour at edges.

### Table 2

| Parameter | Model 1 | Model 2 | Model 3 | Model 4 | Model 5 | Model 6 | Model 7 | Model 8 |
|-----------|---------|---------|---------|---------|---------|---------|---------|---------|
| NLL       | 850.5   | 850.2   | 848.1   | 850.5   | 845.7   | 847.7   | 847.0   | 845.6   |
| Npar      | 3       | 4       | 5       | 5       | 5       | 5       | 6       | 6       |
| AIC       | 1707.0  | 1708.4  | 1704.1  | 1709.0  | 1701.4  | 1705.3  | 1703.9  | 1703.3  |
| $\Delta$AIC$^1$ | 5.6   | 7.1     | 2.8     | 7.7     | 0       | 4.0     | 2.6     | 1.9     |
| $\mu(x)$ (m$^2$ day$^{-1}$) | 28.3   | 29.0    | 27.9    | 26.1    | 24.5    | 25.4    |         |         |
| $\mu_n(x)$ (m$^2$ day$^{-1}$) | 28.9   | 31.1    | 33.3    | 33.5    | 33.4    |         |         |         |
| $\xi (\text{day}^{-1})$ | 0.07   | 0.07    | 0.07    | 0.05    | 0.05    | 0.09    | 0.09    | 0.09    |
| $\xi_n (\text{day}^{-1})$ | 0.07   | 0.07    | 0.07    | 0.05    | 0.05    | 0.09    | 0.09    | 0.09    |
| $\omega$ (m$^{-2}$) | 0.011  | 0.010   | 0.011   | 0.13    | 0.14    | 0.010   | 0.012   | 0.011   |
| $\omega_n$ (m$^{-2}$) | 0.011  | 0.008   | 0.013   | 0.014   | 0.010   | 0.013   | 0.011   | 0.011   |

$^1$Difference in AIC compared to the model with minimum AIC (model 5); Npar: number of parameters; $\mu, \mu_n$: motility (m$^2$ day$^{-1}$); $\xi, \xi_n$: relative loss rate (day$^{-1}$); $\omega, \omega_n$: trapping-efficiency (m$^{-2}$), with the subscripts (n, s) indicate whether the parameter value is for non-starved (n) or starved (s) beetles.
and by preferential behaviour at habitat interfaces. These three models were elaborated with and without accounting for the effect of starvation on beetle behaviour, resulting in a comparison of six model variants.

**Step 3.** In the third step, we determined for the model with the greatest support of the data in the previous step, whether it could be simplified by assuming a common value for motility across subsets of habitats.

**Step 4.** In the fourth and last step, we determined the support of the data for each of the parameters for preference behaviour at interfaces.

The model with the lowest AIC in step 4 was chosen as the most satisfactory model. The confidence intervals for the parameters of this model were derived from log-likelihood profiles (Bolker, 2008). To check the validity of the one-dimensional model we ascertained whether the parameter values of the most satisfactory model calibrated on a one-dimensional representation of the farmland resembled the parameter values of a model that was calibrated to a two-dimensional representation of the farmland. To this end we calculated confidence intervals for parameters of the most satisfactory 1-D model with a $\chi^2$ test (Bolker, 2008) and assessed whether these included the parameter estimates of the 2-D model.

## Results

### Recapture rate and movement distances

In total 865 of the 3,665 marked beetles were recaptured within the 22-day sampling period. Of the recaptured beetles 12.3% had crossed at least one interface, whereas 6.4% had crossed at least two interfaces. Six beetles (0.7%) crossed at least three interfaces. The remaining 80.7% of recaptures were made within the field of release (Table S1).

### Model selection

**Step 1.** In the first model selection step we evaluated the importance of feeding level for motility ($\mu$), relative loss rate ($\xi$) and capture coefficient ($\omega$) of beetles, without accounting for habitat heterogeneity, i.e., using Equation 1. We compared eight models with 3–6 parameters, in which the parameters motility, relative loss rate, and relative recapture rate were estimated for non-starved and starved beetles separately and for non-starved and starved beetles jointly, in all eight possible combinations (Table 2). Lowest AIC was obtained for models 5 and 8, with separate motility and loss rates for non-starved and starved beetles, whereas the AIC was lower for model 5 (no effect of feeding level on capture efficiency) than for model 8 (feeding level affects capture efficiency). Considering the large number of model comparisons that would be made in the subsequent steps and the lack of theoretical support for an effect of feeding level on capture efficiency, it was decided not to consider feeding level effects on capture efficiency further. It should be noted that we cannot make any inferences about lower or higher feeding regimes than the ones we tested.

**Step 2.** Based on the best model in step 1, model 5, we compared six models to determine whether movement behaviour ($\mu$ and $\pi$) was influenced by habitat heterogeneity and feeding level. In this step we calibrated different values of motility ($\mu$) for each of the seven habitats and different values of the preference index ($\pi$) for each of the different interfaces, and in some case different values for each habitat or interface for starved and non-starved beetles. The data gave the greatest support to models that accounted for both differences in motility between habitats and preferential behaviour at habitat interfaces, i.e., both overall hypotheses were supported in the model selection (Table 3). Accounting for differences in motility between habitats and for preferential behaviour at interfaces lowered AIC by 110.8 points if the effect of feeding level was not accounted for (comparing AIC of models 13 and 5) (Tables 2 and 3). This step yielded no support for differences in $\mu$ and $\pi$ between starved and non-starved beetles (Table 3). The only influence of feeding state of the beetles that was retained in the subsequent step was its effect on loss rate $\xi$.

**Step 3.** This step was based on the best model in step 2, model 13. In the third step we assessed whether model 13 could be simplified by assuming a common value for motility across subsets of habitats with similar values for motility (Table 4). Model 18 had the greatest support of the data and lumped motility parameters for margins 1 and 2, fields 1, 3, and 4, and fields 2 and 5, respectively, reducing the number of parameters from 16 in model 13 to 12 in model 18. This reduction in number of parameters gave a reduction in AIC ($\Delta$AIC) of $-4.8$.

**Step 4.** In the final step we assessed the contribution to model fit of parameters describing preferences at habitat interfaces (Table 5). The data supported preference behaviour at each interface, except between field 4 and margin 2 (model 23). Model 23 had the smallest AIC of all models ($\Delta$AIC = $-2$ compared to model 18) and was selected as the most satisfactory model for describing beetle movement over time and space in the field study.

The overall progression of AIC and the number of parameters in the four steps of model selection are...
Table 3  Model selection to test three hypotheses for the effect of habitat heterogeneity (step 2) and feeding level on movement of *Pterostichus melanarius* within a small farmland. Models 10, 12, and 14 assume different behaviour between non-starved and starved beetles

| Hypotheses | Variation in motility between habitats but no preferential behaviour at habitat interfaces | Spatially uniform motility and preferential behaviour at habitat interfaces | Variation in motility between habitats as well as preferential behaviour at habitat interfaces |
|------------|------------------------------------------------------------------------------------------|------------------------------------------------------------------------|------------------------------------------------------------------------------------------|
| Model ID   | 9                                         | 10                                        | 11                                         | 12                                         | 13                                         | 14                                         |
| NLL        | 815.1                                      | 809.1                                     | 798                                        | 793.3                                      | 779.3                                      | 774.2                                      |
| Npar       | 10                                         | 17                                        | 10                                         | 17                                         | 16                                         | 29                                         |
| AIC        | 1650.2                                     | 1652.2                                    | 1616                                       | 1620.6                                     | 1590.6                                     | 1606.4                                     |
| ΔAIC<sup>1</sup> | 59.6                                     | 61.6                                      | 25.4                                       | 30                                         | 0                                          | 15.8                                       |

Parameter

| Parameter | Variation in motility between habitats but no preferential behaviour at habitat interfaces | Spatially uniform motility and preferential behaviour at habitat interfaces | Variation in motility between habitats as well as preferential behaviour at habitat interfaces |
|-----------|------------------------------------------------------------------------------------------|------------------------------------------------------------------------|------------------------------------------------------------------------------------------|
| μ<sub>1</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 39.4                                      | 33.1                                                                 | 90.1                                      |
| μ<sub>2</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 48.2                                      | 99.6                                                                 | 98.6                                      |
| μ<sub>3</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 19.3                                      | 46.8                                                                 | 22.9                                      |
| μ<sub>4</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 55.3                                      | 20.9                                                                 | 25.5                                      |
| μ<sub>5</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 22.4                                      | 39.5                                                                 | 48.0                                      |
| μ<sub>6</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 27.2                                      | 68.8                                                                 | 80.7                                      |
| μ<sub>7</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 4.4                                       | 22.5                                                                 | 44.5                                      |
| μ<sub>8</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 27.2                                      | 24.0                                                                 | 63.6                                      |
| μ<sub>9</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 4.4                                       | 23.7                                                                 | 27.9                                      |
| μ<sub>10</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 24.6                                      | 3.7                                                                  | 30.1                                      |
| μ<sub>11</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 2.9                                       | 2.9                                                                  | 3.5                                       |
| μ<sub>12</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 3.9                                       | 3.9                                                                  | 4.3                                       |
| μ<sub>13</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 5.3                                       | 4.5                                                                  | 6.6                                       |
| μ<sub>14</sub> (x) (m<sup>2</sup> day<sup>-1</sup>) | 4.1                                       | 4.1                                                                  | 9.5                                       |
| p<sub>1</sub> (-) | 0.30                                      | 0.32                                                                 | 0.24                                      |
| p<sub>1,n</sub> (-) | 0.29                                      | 0.08                                                                 | 0.21                                      |
| p<sub>1,s</sub> (-) | 0.29                                      | 0.05                                                                 | 0.24                                      |
| p<sub>2</sub> (-) | 0.08                                      | 0.12                                                                 | 0.07                                      |
| p<sub>2,n</sub> (-) | 0.56                                      | 0.94                                                                 | 0.17                                      |
| p<sub>2,s</sub> (-) | 0.31                                      | 0.45                                                                 | 0.67                                      |
| p<sub>3</sub> (-) | 0.23                                      | 0.25                                                                 | 0.21                                      |
| p<sub>3,n</sub> (-) | 0.25                                      | 0.21                                                                 | 0.22                                      |
| p<sub>3,s</sub> (-) | 0.21                                      | 0.19                                                                 | 0.19                                      |
| p<sub>4</sub> (-) | 0.90                                      | 0.86                                                                 | 0.74                                      |
| p<sub>4,n</sub> (-) | 0.66                                      | 1.03                                                                 | 1.02                                      |
| p<sub>4,s</sub> (-) | 1.03                                      | 0.66                                                                 | 0.74                                      |
| p<sub>5</sub> (-) | 1.60                                      | 0.92                                                                 | 1.21                                      |
| p<sub>5,n</sub> (-) | 2.31                                      | 2.31                                                                 | 2.51                                      |
| p<sub>5,s</sub> (-) | 1.93                                      | 1.93                                                                 | 1.93                                      |
shown in Figure 3. The most important decrease of AIC was achieved during the second step, demonstrating that differences between habitats in motility (μ) and between interfaces in preference (π) had to be accounted for. The third and fourth step were merely refinements to find out whether an equivalent model fit could be obtained with fewer parameters than in the best model identified in step 2.

**Analysis of the most satisfactory model (model 23)**

The confidence intervals of the motility parameters for the three distinguished habitats did not overlap, confirming

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**Table 3** Continued

| Hypotheses                           | Variation in motility between habitats but no preferential behaviour at habitat interfaces | Spatially uniform motility and preferential behaviour at habitat interfaces | Variation in motility between habitats as well as preferential behaviour at habitat interfaces |
|--------------------------------------|------------------------------------------------------------------------------------------|----------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|
| ξn (day⁻¹)                           | 0.053                                                                                    | 0.060                                                                     | 0.059                                                                                           |
| ξs (day⁻¹)                           | 0.054                                                                                    | 0.081                                                                     | 0.080                                                                                           |
| Ω (m⁻²)                              | 0.013                                                                                    | 0.015                                                                     | 0.010                                                                                           |

NLL: negative log likelihood denoting the support of data for the model; Npar: number of parameters; μg(x): motility (m² day⁻¹) in habitat g (=1,...,7); πh: flux-modifier (-) for habitat interface h (=1,...,6); ξ: relative loss rate (day⁻¹), with subscript i indicating non-starved (i = n) and starved (i = s) beetles; Ω: trapping-efficiency (m⁻²).

1 Difference in Akaike information criterion (AIC) compared to the model with minimum AIC (model 13).

**Table 4** Step 3, merging motility parameters among habitats with similar motilities. Four model variants are compared to the full model (13). Grey blocks indicate the different habitats for which the motility parameters were merged into a single parameter

| Parameter | Model 13 | Model 15 | Model 16 | Model 17 | Model 18 |
|-----------|----------|----------|----------|----------|----------|
| NLL       | 779.3    | 779.6    | 779.9    | 780.0    | 780.9    |
| Npar      | 16       | 15       | 15       | 14       | 12       |
| AIC       | 1590.6   | 1589.2   | 1589.8   | 1588.1   | 1585.8   |
| ΔAIC¹     | 4.8      | 3.4      | 4.0      | 2.3      | 0        |
| μ1(x) (m² day⁻¹) | 3.7  | 5.4      | 3.2      | 4.9      | 5.3      |
| μ2(x) (m² day⁻¹) | 6.6  | 6.4      | 6.4      | 6.4      | 6.4      |
| μ3(x) (m² day⁻¹) | 22.9 | 26.0     | 23.2     | 25.0     | 25.0     |
| μ4(x) (m² day⁻¹) | 27.3 | 27.0     | 27.5     | 27.5     | 27.5     |
| μ5(x) (m² day⁻¹) | 100.0 | 100.0    | 100.0    | 62.2     | 60.2     |
| μ6(x) (m² day⁻¹) | 59.4 | 60.2     | 59.5     | 59.5     | 59.5     |
| μ7(x) (m² day⁻¹) | 57.1 | 63.7     | 65.5     | 65.5     | 65.5     |
| π1 (-)    | 0.15     | 0.24     | 0.13     | 0.19     | 0.20     |
| π2 (-)    | 0.10     | 0.10     | 0.10     | 0.11     | 0.11     |
| π3 (-)    | 0.45     | 0.47     | 0.44     | 0.44     | 0.47     |
| π4 (-)    | 0.21     | 0.21     | 0.21     | 0.21     | 0.22     |
| π5 (-)    | 0.86     | 0.82     | 0.86     | 0.87     | 0.81     |
| π6 (-)    | 1.93     | 2.01     | 1.97     | 2.00     | 1.91     |
| ξn (day⁻¹) | 0.059 | 0.059    | 0.059    | 0.058    | 0.061    |
| ξs (day⁻¹) | 0.080 | 0.080    | 0.080    | 0.079    | 0.082    |
| Ω (day⁻¹) | 0.010   | 0.010    | 0.010    | 0.010    | 0.011    |

NLL: Negative log likelihood denoting the support of data for the model; Npar: number of parameters; μg(x): motility in habitat g (=1,...,7); πh: flux-modifier for habitat interface h (=1,...,6); ξ: relative loss rate for non-starved (i = n) and starved (i = s) beetles; Ω: trapping efficiency.

¹Difference in AIC compared to model 18.
their habitat-specificity. In addition, the confidence intervals for three out of five preferential behaviour parameters did not include 1, meaning that in those cases a preference for one of the sides existed.

Calibration of the 2-D Fokker-Planck model version (thus using the full detail of the catch data) yielded parameter estimates that were similar to those of the 1-D model (Table 6), confirming the effectiveness of the 1-D approach for model selection. The only parameter with a large difference between the 1-D and the 2-D models was \( p_2 \). The estimate for the 2-D model, however, remained within the confidence interval of the 1-D model.

**Discussion**

The redistribution pattern of *P. melanarius* that we observed in this field study was most satisfactorily explained by a combination of differences in motility between habitats and preference behaviour at interfaces. The model selection supported both hypotheses (Figure 4): patterns in dispersal are driven by variation in motility between habitats and by preference behaviour at boundaries between habitats. The data gave no support for models that accounted for the initial feeding condition of the released beetles. Motility was lower in the perennial strips than in the crop habitats, which was in agreement with a meta-analysis of literature conducted by Allema et al. (2015). These perennial strips thus acted as barriers to redistribution of beetles across the farmland. Movement at interfaces between crop and perennial vegetation was asymmetric, with beetles preferentially moving towards the crop. The slow movement in the perennial strips compared to the arable land may have been caused by the high vegetation density in the strips, increasing resistance for walking.
Pterostichus melanarius exhibited greatest motility in field 2, with minimum tilled barley, and field 5, with conventionally tilled mustard, estimated at 63.3 m² day⁻¹. Motility was lowest (5.8 m² day⁻¹) in the grassy strip, either with or without a hedgerow. We found no differences in motility among conventional or minimum tilled barley fields 1, 3, and 4 (26.1 m² day⁻¹). At the interface between fields 2 (barley, minimum tillage) and 3 (barley, conventional tillage) and between fields 4 (barley, conventional tillage) and 5 (mustard, conventional tillage), beetles had a preference towards fields 2 and 5, respectively, where the motility was the lowest. This suggests that conditions were better in the latter. For the minimum-till barley field 2 the reason for the attractiveness was not clear, especially in comparison with field 1 where similar agronomic management was applied. In mustard (field 5) we observed a high density of larvae of the turnip sawfly, *Athalia rosae* (L.), that were readily available as food for *P. melanarius* and could explain the preference of beetles for this habitat.

Our model selection procedure did not consider all possible models and can, therefore, not guarantee that the overall best model supported by the data was found. This does not weaken the main conclusion that both habitat-specific motility and preference behaviour at habitat interfaces are necessary to describe movement of a predatory beetle in a heterogeneous environment. Furthermore, the finally selected model showed a satisfactory description of the data (see also Figure S1).

Differences between habitats in movement pattern, movement rate, displacement distance, or rate of population spread have been attributed to habitat preference (Wallin, 1986), prey availability (Bommarco & Fagan, 2002), plant density (Thomas et al., 2006), and land use intensity (Kennedy, 1994). Within arable landscapes, differences in movement were attributed to activity density (Holland et al., 2004) and aphid (prey) density in combination with feeding level of beetles (Wallin & Ekbom, 1994). In comparisons between adjacent habitats, significant bias in movement direction has been observed (Duelli et al., 1990; Kujawa et al., 2006; Thomas et al., 2006; Allema et al., 2014). Hedgerows and grass margins appeared to be barriers for movement of carabids (Thomas et al., 1998; García et al., 2000) and the permeability

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**Table 6** Comparison of parameter values of the most satisfactory model optimized for the one-dimensional (1-D) representation of the farmland (model 23) and for the original two-dimensional (2-D) farmland. For the most satisfactory model in the 1-D farmland the 95% confidence margins are shown in parentheses.

| Parameter | 1-D | 2-D |
|-----------|-----|-----|
| NLL       | 782.8 | 1438.7 |
| Npar      | 11 | 10 |
| \( \mu_M(x) \) (m² day⁻¹) | 5.8 (3.4–14.0) | 7.2 |
| \( \mu_L(x) \) (m² day⁻¹) | 26.1 (21.0–33.0) | 21.9 |
| \( \mu_H(x) \) (m² day⁻¹) | 63.3 (48.0–86.0) | 50.2 |
| \( \pi_1 \) (-) | 0.22 (0.10–0.39) | 0.39 |
| \( \pi_2 \) (-) | 10.0 (4.8–20.0) | 7.69 |
| \( \pi_3 \) (-) | 0.45 (0.15–1.15) | 0.47 |
| \( \pi_4 \) (-) | 0.23 (0.14–0.4) | 0.31 |
| \( \pi_5 \) (-) | 0.53 (0.30–0.91) | 0.50 |
| \( \xi_n \) (day⁻¹) | 0.058 (0.04–0.076) | 0.063¹ |
| \( \xi_s \) (day⁻¹) | 0.079 (0.06–0.10) | |
| \( \phi \) (day⁻¹) | 0.010 (0.007–0.014) | 0.119 |

NLL: Negative log likelihood denoting the support of data for the model; Npar: number of parameters; \( \mu_M(x) \): motility in the margins; \( \mu_L(x) \): motility in fields 2 and 5; \( \mu_H(x) \): motility in fields 1, 3, and 4; \( \pi_1 \): flux-modifier for habitat interface \( h = 1, ..., 6 \); \( \phi \): trapping efficiency; \( \xi_n, \xi_s \): relative loss rate, with subscript n or s indicating the parameter value for non-starved (n) and starved (s) beetles.

¹Excessive calculation time necessitated simplifying the 2-D model by using a global parameter for relative loss rate. For description of parameters see Table 1.

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**Figure 4** Summary of the most satisfactory model, shown in the setting of the field. \( \mu \): motility; \( \pi \): flux-modifier for habitat interface indicated by the arrow. [Colour figure can be viewed at wileyonlinelibrary.com]
of these margins was related to the degree of saturation of the beetles (Frampton et al., 1995; Mauremooto et al., 1995). Our study confirms that strips with perennial species have much lower motility than arable fields (Figure 4), i.e., they act as barriers to movement. Furthermore, we found beetles to have 4× greater preference for crops over perennial strips, but we found no evidence for an effect of initial feeding level on edge behaviour. This suggests that the decision to leave a habitat is determined by external signals rather than by the beetle’s internal state (Allema et al., 2008), at least at the level of food deprivation achieved in this study.

In the literature, movement of insects across heterogeneous landscapes has been addressed using various mathematical frameworks, but mostly by diffusion. Turchin (1998) argued that for ecological phenomena, the Fokker-Planck framework is the most appropriate because it allows for heterogeneous densities across space in the steady state if movement behaviour differs among habitats. We have adopted this framework in a discrete time model and added to it preferential behaviour at habitat interfaces using flux-modifiers. Other studies have used continuous time diffusion approaches instead, e.g., Maciel & Lutscher (2013) and Ovaskainen & Cornell (2003). These authors analysed the consequences of choice behaviour at the boundary for crossing the boundary. In our study, we did not consider behaviour at the boundary itself, but instead we considered the fluxes across the boundary. This approach was chosen to address the question whether differential movement across boundaries, in addition to differences in motility among habitats, was required to explain redistribution dynamics. The approaches of Maciel & Lutscher (2013), Ovaskainen & Cornell (2003), and ours are similar but they are not identical. Further work is needed to address how these different approaches are related to each other, particularly at the habitat interface.

The values for motility that we found in this study are consistent with those found for other carabid species (Allema et al., 2015). With motility we can assess the area that organisms may explore during a given period and thus the spatial extent of their habitat use (Allema et al., 2015). Motility in crop habitats varied from 26 to 63 m² day⁻¹. The distribution of beetles from a hypothetical point release would thus have a variance of 4 × 26–63 m² after 1 day, i.e., 104–252 m². When taking the square root, this translates to a distribution with a standard deviation of 10–16 m. For a growing season of 14 weeks and assuming a constant rate of dispersal, the variance would be 14 × 7 × 104–252 m², i.e., 5 000–25 000 m², representing a 2-D bell shape with a standard deviation of 100–160 m. These values are similar to the range of 2–7 ha that Firle et al. (1998) estimated for P. melanarius based on individual movement behaviour obtained by tracking individual movements in the field. Thus, the estimates of population spread of this study are consistent with those in the literature, while providing further information on the effect of habitat transitions.

Conclusions

This study demonstrates that differences in motility between habitats and preferential behaviour at habitat interfaces affect the redistribution of P. melanarius in a small farmland. Perennial vegetation strips acted as barriers for redistribution of P. melanarius. At the interface between a perennial strip and a crop, beetles preferred to move into the crop. Predators in fields surrounded by perennial strips will thus spend more time in the crop where they can feed on prey and contribute to biological pest control. We found that crop species and tillage are not sufficient to explain the time P. melanarius will spend in a habitat. Further studies should therefore consider factors such as prey availability and shelter in addition to crop management. Designing pest suppressive farmland based on individual species’ behaviour awaits more insight in the effects of habitat characteristics on motility and preference behaviour at habitat interfaces.

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Data availability statement

All data underlying the findings described in the paper are fully available without restriction at the data archive of the Royal Netherlands Academy of Arts and Science. The
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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Equation S1. Key equations of the dynamical models that were fitted to the data.
Table S1. Number of beetles recaptured per habitat as a function of release site (fields 2, 3, or 5; see Figure 1) and feeding level (non-starved vs. starved). Number of released beetles between parentheses.
Figure S1. Cumulative number of recaptured beetles (observed, o; predicted, drawn line) through time at each recapture point in the 1-D representation of the landscape. The x-coordinate of the recapture point is shown above each panel. The error bars represent the 95% confidence intervals of the observations.