

Quantifying and simulating movement of the
predator carabid beetle *Pterostichus*
melanarius in arable land

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This research was conducted under the auspices of the C. T. de Wit Graduate School of
Production Ecology and Resource Conservation

Quantifying and simulating movement of the
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Thesis

submitted in fulfilment of the requirements for the degree of doctor

at Wageningen University

by the authority of the Rector Magnificus

Prof. Dr M.J. Kropff,

in the presence of the

Thesis Committee appointed by the Academic Board

to be defended in public

on Tuesday 13 May 2014

at 4 p.m. in the Aula.

Bas Allema

Quantifying and simulating movement of the predator carabid beetle *Pterostichus melanarius*
in arable land, 134 pages.

PhD thesis, Wageningen University, Wageningen, NL (2014)

With references, with summaries in Dutch and English

ISBN 978-90-6173-910-0

Abstract

Biological control provided by entomophagous arthropods is an ecosystem service with the potential to reduce pesticide use in agriculture. The distribution of entomophagous arthropods and the associated ecosystem service over crop fields is affected by their dispersal capacity and landscape heterogeneity. Current knowledge on entomophagous arthropod distribution and movement patterns, in particular for soil dwelling predators, is insufficient to provide advice on how a production landscape should be re-arranged to maximally benefit from biological pest control. Movement has mainly been measured in single habitats rather than in habitat mosaics and as a consequence little information is available on behaviour at habitat interfaces, i.e. the border between two habitats.

This study contributes to insight into movement patterns of the entomophagous arthropod *Pterostichus melanarius* (Illiger) in an agricultural landscape as a knowledge basis for redesign of landscapes for natural pest control. Movement patterns were studied with video equipment in experimental arenas of 5 m² and with mark-recapture at much larger scales in the field. Interpretation of the results was supported by diffusion models that accounted for habitat specific motility μ (L² T⁻¹), a measure for diffusion of a population in space and time, and preference behaviour at habitat interfaces.

Movement of carabids has mostly been quantified as movement rate, which cannot be used for scaling-up. Available information on movement rate of carabids was made available for scaling-up by calculating motility from published data and looking for patterns through meta-analysis of data from thirteen studies, including 55 records on twelve species. Beetles had on average a three times higher motility in arable land than in forest/hedgerow habitat. The meta-analysis did not identify consistent differences in motility at the individual species level, and a grouping of species according to gender or size did not demonstrate a significant gender or size effect.

A methodology to directly estimate motility from data using inverse modelling was evaluated on data of a mass mark-recapture field experiment in a single field of winter triticale (*x Triticosecale* Wittmack.). Inverse modelling yielded the same result as motility calculated from squared displacement distances. In the first case, motility was calculated as an average over motility of individuals, in the second case motility was estimated from a population density distribution fitted to the recapture data. The similarity in motility between these two very different approaches strengthens the confidence in motility as a suitable concept for quantifying dispersal rate of carabid beetles, and in inverse modelling as a method to retrieve movement parameters from observed patterns.

The effect of habitat heterogeneity on movement behaviour was studied for *P.*

melanarius across adjacent fields of oilseed radish (*Raphanus sativus*) and rye (*Secale cereale*) in a mark-recapture experiment. The field study was complemented by observations on movement behaviour in the experimental arena. Motility was neither significantly different between the crop species in the field nor in the arena. Overall movement in the field was significantly affected by behaviour at the interface between the crops. Beetles moved more frequently from rye to oilseed radish than in the opposite direction. The arena data indicated greater frequency of habitat entry into oilseed radish as compared to rye. Analysis of video tracking data from the arena resulted in estimates of motility that, when scaled up were close to those obtained in the field. Thus, the studies at the smaller and larger scales gave qualitatively and quantitatively similar results.

The effect of habitat heterogeneity on within-season dispersal behaviour was further explored in an agricultural landscape mosaic comprising perennial strips and different crop species with distinct tillage management. Semi-natural grass margins were functionally different from the crop habitats. Motility was lower in margins than in crop habitats, and at the crop-margin interface more beetles moved towards the crop than to the margin. Margins thus effectively acted as barriers for dispersal. In the crop habitats motility differed between fields but no consistent relations were found with crop type, food availability or tillage. Based on the motility in crop habitats *P. melanarius* was predicted to disperse over a distance of about 100 – 160 m during a growing season in a landscape without semi-natural elements. Given this range little redistribution of beetles is expected between fields within a growing season, even more when fields are surrounded by grass margins or hedgerows, meaning that the success of biological control by this species is more dependent on field management affecting local population dynamics than on habitat heterogeneity.

This thesis has resulted in a methodological approach to quantify dispersal behaviour of ground-dwelling insects from mark-recapture data in heterogeneous environments using inverse modelling. The combination of models and data proved to be powerful for studying movement and contributes to the development of predictive dynamic models for population spread of entomophagous arthropods. These models for population spread may be used as part of multi-objective assessment of alternative landscape configurations to find spatial arrangements of land use that maximize the ecosystem service of biological control as part of a wider set of landscape functions.

Keywords: landscape entomology, movement ecology, quantifying movement, population spread, habitat heterogeneity, motility, edge-behaviour, diffusion model, model selection, inverse modelling, Pterostichus melanarius, Carabidae, entomophagous arthropod

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Chapter 1

General introduction

1 Biodiversity decline and loss of ecosystem functions

Expansion and intensification of agricultural production has caused a sharp decline in the number of species inhabiting agricultural landscapes at all trophic levels in the past fifty years. The loss of biodiversity has negative consequences for the regulation of ecological processes such as nutrient cycling, pollination and pest control. With the decline of the ecosystem service of natural pest control agriculture became increasingly dependent on the use of pesticides, resulting in the so called pesticide treadmill and the creation of secondary pests (Bosch 1980). Pesticide resistance has become an ubiquitous problem, as have the environmental and human health threats associated with pesticide transfers to water, soil and air (Matson et al. 1997). Clearly this is not a sustainable form of pest control even less so in the context of an increasing demand for food production. The use of ecologically based management strategies can increase the sustainability of agricultural production while reducing off-site consequences (Matson et al. 1997). Conservation biological control – the actions taken to protect and maintain established populations of natural enemies in a given area – is one of the solutions for sustainable control of insect pests. The diversity of the whole cropping system plays herein an important role. This includes the diversity of crops in space, their sequence through time, the diversity of non-crop habitat and the spatial arrangement and spatial dimensions of land-uses. The compositional and configurational heterogeneity, i.e. variation in and spatial arrangement of land use (Turner 2005), determines the spatial distribution of insects in the landscape. However, the current knowledge on insect distribution patterns is insufficient to advise on how a production landscape should be arranged to maximize profit from conservation biological control. An important component that is missing is information on the dispersal behaviour of predatory insects, which play an important role in conservation biological control. Dispersal of predators in heterogeneous landscapes is often studied with simulation models but the empirical foundation for these models is weak. This study contributes insights on dispersal behaviour of predatory insects in an agricultural landscape to provide a basis for the redesign of landscapes for natural pest control.

2 Theoretical background

The research aim of my project was to study dispersal behaviour of an insect predator in an agricultural environment in a quantitative way. We chose a predatory carabid beetle as the model organism. Much of what we know about carabid dispersal behaviour comes from

theoretical studies. Here I summarize three of these studies to illustrate how models of dispersal in carabid beetles have recently been used.

Westerberg et al. (2005) studied the effect of changing landscape composition (the proportion of favourable and unfavourable habitats) and configuration (the spatial clustering of favourable habitats) on the population distribution of *Poecilus cupreus* using a model in which dispersal behaviour depended on the quality of the habitats only, and, thus did not consider the effect of interfaces between habitats and demographic variables of the predator. Their model showed that equilibrium densities were reached within one predator generation and, thus, that dispersal alone could explain population distribution patterns. In the model of Westerberg et al. (2005) arable fields were associated with a low habitat quality and a high movement rate compared to perennial ley that was associated with a high habitat quality and a low movement rate. Their model showed that, from a biological control point of view, a uniform distribution of high quality habitats is preferable as this will yield the highest densities of beetles in arable fields. The model also showed that the contrast in habitat quality (i.e. differences in movement rate between habitats) had a large influence on population aggregation and resource use efficiency in the preferred habitats. Contrasts in habitat quality might, thus, be an important parameter to take into account when designing landscapes for optimal biological control. The classification of habitats into annual or perennial habitat is a simplification of the real heterogeneity. Whether landscape heterogeneity can be simplified to perennial and annual habitats to describe beetle movement will be investigated in chapter 5.

Sherratt and Jepson (1993) studied the relation between landscape configuration and population dynamics for a landscape composed of a matrix of arable fields that were regularly, but not simultaneously, sprayed with pesticides. Parameter values were chosen to reflect the dispersal rates and pesticide susceptibility of carabids. The simulation time was 5 years, during which the individuals reproduced at regular time intervals. The dispersal rate was dependent on the density of prey and was higher in fields with less prey, which is similar to the low quality habitat in the study of Westerberg et al. (2005). To a certain degree, beetles were reluctant to cross boundaries irrespective of the direction they came from. The authors found that the speed of dispersal of the predators across field boundaries, which was determined by the dispersal rates within fields, boundary permeability and field size, was an important factor influencing the persistence of predator populations. Furthermore, there appears to be an optimum dispersal rate or boundary permeability that maximizes the range of conditions under which natural enemies persist.

Benjamin et al. (2008) evaluated the effect of landscape composition and configuration on the spatial population dynamics of *P. melanarius* during a period of 20 years for a series of realistic landscapes consisting of arable land and semi-natural habitat. Dispersal rates between habitats were calculated from a simplified process model at the field level using the surface area and perimeter of fields and the probability to leave a habitat as input parameters. Based on this model the authors concluded that local demography (survival and reproduction) played the main role in governing the dynamics and population viability of *P. melanarius* in all landscape configurations.

It is obvious that dispersal behaviour played a different role in these three models. Westerberg et al. (2005) stressed the importance of dispersal behaviour to explain patterns of population density within a generation. Sherratt and Jepson (1993) showed that dispersal behaviour is important for the viability of carabid populations in a landscape with frequent disturbances. Benjamin et al. (2008), on the contrary, demonstrated that local demography, and not dispersal, is most important for viability of carabid populations. The model of Benjamin et al. (2008) is the most complete in that it includes population dispersal, demography and seasonality, but the empirical foundation for the dispersal function was rather weak.

In the three theoretical studies mentioned above the landscape was classified into a suitable and less suitable habitat, each with a different dispersal rate. Westerberg et al. (2005) distinguished between annual and perennial crops, Sherratt and Jepson (1993) determined habitat suitability based on prey density and Westerberg et al. (2005) distinguished between arable fields and semi-natural habitat. In reality all these components of heterogeneity are present simultaneously but it is not yet clear how important they are for describing beetle dispersal in space.

3 Dispersal, movement, motility and population spread

Dispersal is the displacement of organisms in space and can be described at different temporal and spatial resolutions. The dispersal power of an organism may be expressed by its maximum velocity. Wallin and Ekbohm (1994) recorded a sprint speed for *P. melanarius* of $3.0 \pm 0.5 \text{ m min}^{-1}$ (mean \pm sd) on a smooth surface. When walking in one direction *P. melanarius* may thus cover large distances in a short time. The average daily displacement distance, however, is in the order of several meters per day (Wallin and Ekbohm 1988,

Thomas et al. 1998) due to frequent stops and burrowing behaviour (Firle et al. 1998), and because the walking path is often not straight but may follow seemingly random directions. The daily average displacement distance is a misleading parameter because it presupposes a linear increase in dispersal distance with time, while dispersal distance, as a result of random movement, increases quadratically with time (Turchin 1998, Codling and Plank 2010). The motility parameter describes dispersal based on a quadratic increase of distance, or surface area, in time, and resembles more closely the process of dispersal than the daily displacement distance does. Motility ($\text{m}^2 \text{d}^{-1}$) is similar to the diffusion constant and can be calculated from turning angles and move lengths of the beetle, or can be estimated from a diffusion model fitted to population redistribution data (Turchin 1998). When multiplied by four, motility describes the rate of population expansion in space. A motility of $10 \text{ m}^2 \text{d}^{-1}$ will thus result in a population expansion area of 40 m^2 per day. The motility parameter has only occasionally been estimated for carabid beetles. Thomas et al. (1998) reported a motility for *P. melanarius* of $26 \text{ m}^2 \text{d}^{-1}$ in cereals. On a larger time scale than days, dispersal can be expressed as a range of population spread. Using an individual based model Firle et al. (1998) estimated a range of population spread of *P. melanarius* of 2-7 ha after a growing season of 14 weeks, depending on the probability of switching between resting and walking behaviour.

4 Dispersal over habitat edges

Baars (1979) and Rijnsdorp (1980) were among the first to study movement of carabids over habitat edges. Baars (1979) found no indication that beetles respond to an edge between suitable and unsuitable habitats and assumed that beetles readily move to a suitable habitat due to more directed movements in the unsuitable habitat. Rijnsdorp (1980) came to a different conclusion and supported the idea that beetles actively choose to cross an edge between unsuitable and suitable habitats. Results from large-scale mark-recapture experiments with *P. melanarius* revealed extensive population exchange within and between two fields planted with wheat and beans (Thomas et al. 2006). Movement from wheat to beans was 3-6 times greater than vice versa. In a similar mark-recapture experiment on two fields of winter barley separated by a hedgerow, only a small percentage of the population of *P. melanarius* moved between fields (Thomas et al. 1998). Field boundaries may thus play an important role in population distribution of *P. melanarius* between fields.

5 Biology of the model species *P. melanarius* and its contribution to pest suppression

Pterostichus melanarius (Illiger) (13-17 mm, Luff 2007) is a characteristic inhabitant of arable fields in Europe (Thiele 1977) and is considered a true inhabitant of cereals (Wallin 1987). On Dutch arable land *P. melanarius* is among the twelve “core” species that are very common (Turin and van Alebeek 2007). The adult beetles emerge from pupae in late spring with sudden peaks of abundance in June-July (Turin 2000) from the centre of cultivated areas, rather than from uncultivated areas (Wallin 1987, Noordhuis et al. 2001). Densities are in the range of 0.05-29 beetles per square metre (Holland et al. 2007). Reproduction takes place from early July till early September (Holland et al. 2007). Eggs are oviposited under experimental conditions at a rate of 3.0 ± 2.1 or 28.2 ± 17.4 (mean \pm sd) eggs per three days (Wallin et al. 1992) depending on the diet. The eggs are laid in small quantities (Wallin 1987) at a low depth in relatively moist soil near stems of plants (Tréfás and Van Lenteren 2008). The average number of eggs laid per female during her life time under experimental conditions was 134 (Tomlin 1975) or 174 (Desender et al. 1985). However, variation in egg production is high between females (Desender et al. 1985). The sex-ratio is close to one, except at the beginning of the reproduction period when males predominate (Desender et al. 1985). The beetles develop from egg to adult in about 320 days (Aukema et al. 1996). About 30% of the adults that take part in reproduction have already reproduced in the previous year (Turin 2000). Adult life span can be up to four years (Wallin 1987). Overwintering of adult beetles takes place predominantly in cultivated rather than semi-natural areas. Sotherton (1984) found the highest overwintering densities of adults and larvae in fields sown with winter wheat compared to other habitats including field boundaries and woodland. *Pterostichus melanarius* predominantly moves by walking rather than flying (Wallin 1985).

Pterostichus melanarius is for 90% carnivorous and eats a broad range of epigeal invertebrates (Turin 2000), including at least fourteen pest species belonging to Mollusca, Coleoptera, Diptera, Homoptera and Lepidoptera (Sunderland 2002). A review by Symondson et al. (2002) of manipulative field studies showed that in ~75% of the cases generalist predators, whether single species or species assemblages, reduced pest numbers significantly. The role of *P. melanarius* as a single species in reducing pests in the field has been demonstrated for slugs and aphids. Sydmonson et al. (1996) and Bohan et al. (2000) found evidence that *P. melanarius* aggregated in patches of high slug density and then reduced slug abundance in those patches to a significant degree by predation. Winder et al. (2001) obtained negative regressions between the density of *P. melanarius* and the rate of

increase of the aphids *Metopolophium dirhodum* and *Sitobion avenae* during the early stages of population development, which Winder et al. (2005) attributed to predation by *P. melanarius* on the aphids.

6 Motivation and research objectives

The motivation for this thesis was the need for insight in dispersal of insect predators within and across habitat interfaces to support design of pest-suppressive landscapes. In this thesis I focused on dispersal behaviour of the generalist predator *Pterostichus melanarius* (Coleoptera: Carabidae). My research objectives were:

1. To develop an experimental system to study walking behaviour under semi-natural conditions;
2. To study dispersal behaviour in terms of movement behaviour motility and interface-mediated behaviour;
3. To identify components of landscape heterogeneity that are relevant for describing dispersal and;
4. To relate population spread to individual movement behaviour.

To reach these objectives experiments were conducted in which measurements were made on movement behaviour, motility and edge-behaviour. The research topics investigated and the chapters in which they are presented are shown in Table 1.

Table 1 Overview of the research topics that are studied on movement behaviour, motility and edge-behaviour and the chapters in which they are presented.

Obj. 1	Obj. 2				Obj. 3	Obj. 4
Light quality	Satiation level	Species identity	Habitat type	Beetle sex	Landscape heterogeneity	Scaling
Movement behaviour	II	IV	IV	II, IV		IV
Motility	V	III	III, IV, V	III	V	
Edge behaviour	V		IV, V			

7 Thesis outline

The relations between the chapters with experimental results are shown in Fig. 1. In chapter two the experimental setup was developed for behavioural observations on movement behaviour which was needed for scaling up movement behaviour to population spread in chapter four. In chapter three the methodology was developed for estimating motility from mark-recapture data using a Fokker-Planck diffusion model and was tested for a homogeneous environment. In chapter four the Fokker-Planck model was extended with a parameter for the preference of beetles at habitat interfaces and was applied to an environment existing of two habitats. Finally, in chapter five, the methodology was used to understand dispersal in a heterogeneous landscape. The content of the various chapters is outlined in more detail below.

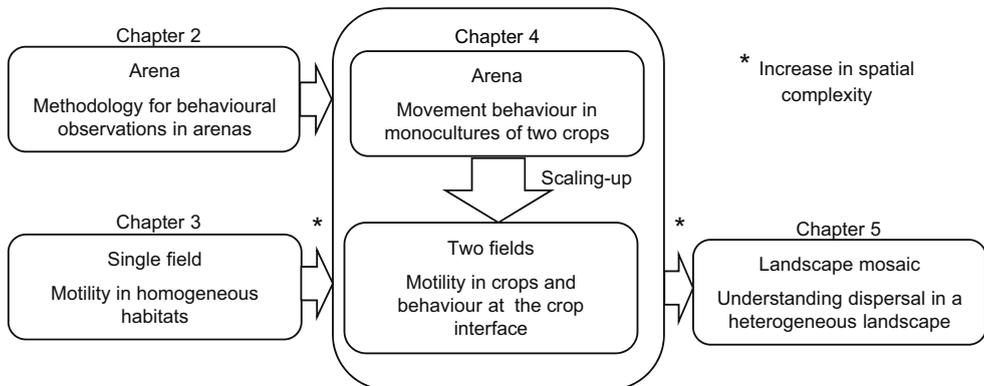


Fig. 1 Diagram showing the relations between the chapters with experimental results.

In **chapter two** I developed the experimental setup that was used in chapter four to link movement behaviour to population spread. Movement behaviour was recorded with cameras in arenas of 5 m². Beetles were visible by attaching a retro-reflector to the elytra and placing a radiation source close to the camera. In earlier studies red light was used to enable observation, but it was unclear if this could affect movement behaviour. To investigate this I compared movement behaviour under red, white and near infrared radiation.

In **chapter three** I explained why I prefer to quantify dispersal in terms of motility, instead of the frequently used mean dispersal distance. I approximated motility from mean dispersal distances reported in literature and used this overview on motility values for a meta-analysis to see if there are consistent differences in motility between carabid species or between

habitat types. In the second part of the chapter a software application was developed to estimate motility from mark-recapture data along with parameters for loss rate and trapping efficiency. I tested the application on a mark-recapture data set with *P. melanarius* in a homogeneous environment.

In **chapter four** landscape complexity was increased to an environment consisting of two adjacent crops. I wanted to know if dispersal between the crops was influenced by a crop interface and/or by habitat specific motility. Next to the field experiment I studied movement behaviour in laboratory arenas planted with the same crops as in the field to get more insight into the relation between movement behaviour and population spread.

In **chapter five** landscape complexity was further increased to the scale of agricultural fields separated by semi-natural elements. The compositional heterogeneity of this landscape mosaic comprised of cultivated and uncultivated areas, differences in crop species, tillage regimes and food availability. My aim was to identify the components of landscape heterogeneity that are relevant for describing dispersal.

In the **final chapter**, I summarize the main results of this thesis and discuss the relation between landscape heterogeneity and carabid beetle population distribution. I highlight the implications of this work with respect to previous work and provide recommendations for future research in this area.

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Chapter 2

Effect of light quality on movement

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Eveliëne Steingröver and Joop van Lenteren

Abstract

Behaviour of nocturnal insects is routinely observed under red light, but it is unclear how the behaviour under red light compares to behaviour in complete darkness, or under a source of white light. Here we measure movement behaviour of the nocturnal carabid beetle *Pterostichus melanarius* Illiger (Coleoptera: Carabidae) using camera recording under a near infrared (nir), red or white radiation source. Red light significantly reduced movement speed in females similar to the effect of white light and different from nir. Also movement activity and pause length were affected by radiation source, with a significant difference between nir and white light, and with intermediate values in red light. The results presented here indicate that *P. melanarius* has different movement behaviour under the three radiation sources and suggest that nir rather than red radiation is most appropriate for measuring behaviour in total darkness. However, in the field total darkness is rare both because of natural light sources such as the moon and stars but increasingly also due to ecological light pollution, and therefore red light may still be of use for observing ecologically and practically relevant natural night time behaviour.

1 Introduction

Carabid beetles are important providers of ecosystem services in agriculture by feeding on insect pests, slugs as well as weed seeds (Kromp 1999; Sunderland 2002; Westerman et al. 2003). Behaviour of carabid beetles has therefore been studied extensively, in particular to explain how carabids can aggregate in patches of high pest density and contribute to density dependent regulation (Mols 1993; Firlie et al. 1998; Holland et al. 2004). Behaviour of nocturnal carabid beetles, like other nocturnal insects, is often studied in red light (620-750 nm) (e.g. Brunsting 1982; Heise 1992) because red light is visible to the observer, but assumed to be invisible to the insect (Ottesen 1990; Heise 1992; Gibson 1995; Depickère et al. 2004; Turnbull and Barmuta 2006; Guy et al. 2008). Electro-physiological studies, however, have shown red light receptors in Odonata, Hymenoptera, Lepidoptera and Coleoptera (Briscoe and Chittka 2001; Crook et al. 2009). Behavioural experiments have shown red light sensitivity in Ephemeroptera (Heise 1992), Diptera (Green and Cosens 1983; Gibson 1995), Plecoptera (Turnbull and Barmuta 2006), Lepidoptera (Zaccardi et al. 2006) and Hymenoptera (Reisenman and Giurfa 2008). The question then arises whether observations under a red radiation source represent night time behaviour.

There are only few studies on the effect of red light on behavioural components such as movement speed or direction in insects. Griffiths et al. (1985) exposed the nocturnal carabid beetle *Agonum dorsale* to a flash of white or red light. In white light beetles sought shelter, while in red light no such response was observed. This observation suggests that nocturnal behaviour may be retained under red light. However, these authors did not study long duration exposure to red light. Heise (1992) demonstrated that mayfly nymphs (*Stenacron* spp.) stayed further away from a red light source compared to a situation with infrared radiation. Depickère et al. (2004) demonstrated that red light affects aggregation behaviour in the ant *Lasius niger* inside the nest. Overall, support for the assumption that insects are insensitive to red light appears rather weak.

As a prelude to studies on nocturnal movement behaviour of *Pterostichus melanarius* Illiger (Coleoptera: Carabidae) under different conditions of substrate and food availability, we conducted a study on the effect of experimental illumination technique, comparing behavioural components under red, white and near infrared radiation. We show that radiation source affects several behavioural parameters, such as movement speed, movement activity and pause length.

2 Materials and methods

2.1 Insects

Pterostichus melanarius was collected from an organic cereal field of the Wageningen University Farm Droevendaal (Wageningen, the Netherlands) during the summer of 2008 and kept in containers with sufficient food and water. Seven days before the start of measurements, individual beetles were transferred to Petri-dishes and fed with fly maggots (*Lucilia caesar*) for two hours, long enough to be satiated (Mols 1993). The beetles were subsequently kept in Petri-dishes with a layer of moist gardening peat soil in a climate chamber (L11:D13; 20/12°C) for five days. Light was provided by fluorescent tubes. Two days before recording, beetles were again fed with maggots for two hours. One day before recording started, beetles were released in the experimental arenas to acclimatize to the conditions in the greenhouse. The arenas measured 37 x 56 x 7 cm and were filled with a layer of moist gardening peat soil.

2.2 Experimental design

The experiments were conducted in the beginning of October in two identical climate regulated greenhouse compartments at a temperature of 20 °C during the light period (8 a.m. – 7 p.m.) and 15 °C during the dark period (7 p.m. – 8 a.m.). During the dark period the compartments were blinded with black screens which excluded all outside light. In each experimental session, movement behaviour was compared between two radiation sources in the two separate compartments (i.e. red-nir, red-white, or nir-white). In each compartment 12 beetles were recorded simultaneously from 7 p.m. till 7 a.m. for a recording period of 20 minutes per hour. The total time length of recording was $12 \times 20 = 240$ min. Experimental sessions were replicated resulting in $2 \times 2 \times 12 = 48$ beetles (24 males and 24 females) per treatment, except for the white treatment for which only 47 beetles (17 males and 30 females) were available. Beetles that died during the observations (2 in nir and 3 in red) were replaced. Due to loss of mark (1 in red, 5 in nir and 4 in white) and bad image quality in white (12), the eventual number of usable beetle tracks were 47 (24 males and 23 females) in red light, 43 (16 male and 27 females) in nir radiation, and 31 beetles (17 males and 14 females) in white light. Treatments will be abbreviated as: red, nir and white.

2.3 Observations

Images were captured using an analogue monochrome camera (Ikegami, ICD-49E) at 5 frames per second and a resolution of 768x576 pixels. The near infra-red cut filter was removed from the camera to make it sensitive to nir. An auto-adhesive retro-reflector (35

mm², ~5 mg; 3M8850, 3M, Leiden, The Netherlands) was attached to the elytra of each beetle (see picture a in the appendix). A retro-reflector reflects the radiation back in the direction of the source and is therefore highly visible even at low radiation intensity. Radiation sources were placed next to the camera (for red and nir) or 1.5 m above the camera (for white). Red light was provided by a custom made array of 28 red leds (Luxeon III, LXHL-PD09, 620.5 – 645 nm) (Farnell, Utrecht, The Netherlands) placed next to the camera. Nir radiation was provided by a commercially available led array (IR-880/12, 880 nm) (c-tac, Winsen, Germany). White light was provided by an Agro SON-T lamp (600 W, 320-780 nm), yielding a net radiant flux of 12 W m⁻² at the level of beetles. For red and nir, radiant fluxes were negligible (< 0.1 W m⁻²).

2.4 Data processing

Object detection software Ethovision 3.1 (Noldus Information Technology, Wageningen, The Netherlands) was used to extract movement tracks from the image files. Movement track data were analysed in Matlab R2009a (The MathWorks) by a self-written program. Beetles tended to track arena edges upon encounter. We excluded from analysis all data records representing beetle positions within 3 cm from the edge of the arena. The first characteristic of behaviour is the time spent in the arena's interior, which is simply the time span covered by positions that are more than 3 cm from the arena edge. The second characteristic is the percentage time when in the arena's interior during which beetles were not visible and assumed to be hiding in the soil. The third characteristic is movement activity, defined as the percentage time beetles were visible and walking when in the arena's interior. The fourth characteristic is the percentage time beetles were visible but not walking when in the arena's interior. During periods of movement activity, behaviour was further characterized by movement speed, pause length, pausing frequency and angular dispersion of turning angles. To obtain these characteristics position data in the arena's interior were aggregated into moves, using a data reduction process described by Turchin (1998, p. 132).

A move was created from position i to position n if the beetle moved a set minimum distance and all intermediate positions were at a distance $\leq \Delta z$ from the line segment connecting positions i and n (Fig. 1). The value Δz was set at 0.4 cm, which is the size of a pixel, so that maximum detail of the paths was retained. The minimum move length was set to the average body length of *P. melanarius*: 1.7 cm. To avoid track interpolation over large gaps, a new move was started when a beetle was not visible for more than 2 sec.

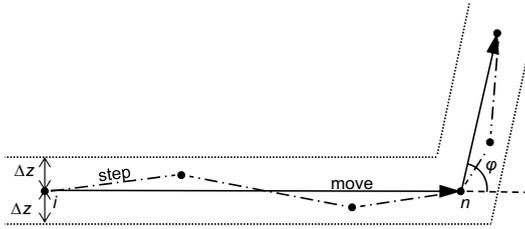


Fig. 1 Steps are displacements between two successive measured spatial positions. A move is created from the successive positions i to n when all intermediate positions have a distance $\leq \Delta z$ from the line connecting i and n . Turning angle (φ) is the difference in heading between two subsequent moves.

For each move, the move length, duration, speed, heading (i.e. absolute direction in the plane: $0 - 2\pi$) and turning angle (change in direction from one move to the next within the interval: $-\pi, \pi$) were calculated. Periods without movement longer than 2 sec were denoted as pauses. Pauses shorter than 2 sec were included within a move.

Angular dispersion of turning angles was calculated for each beetle as mean vector length r , according to:

$$r = \frac{1}{m} \left[\left(\sum_i \cos \varphi_i \right)^2 + \left(\sum_i \sin \varphi_i \right)^2 \right]^{1/2}$$

in which m is the number of turning angles, and φ_i turning angle in radians between move i and $i+1$ (Batschelet 1981). A large angular dispersion (small vector length) indicates frequent large changes in heading whereas low dispersion (large vector length) indicates a tendency to straight walk.

2.5 Statistical analysis

The measurements on moves were aggregated per beetle for the statistical analysis. The assumption of homoscedasticity was violated for all variables restricting us to non-parametric statistics. Fisher's exact test (GenStat Thirteenth Edition, VSN International Ltd) was used to test for differences between treatments in proportion of beetles that moved at least once during the observation period. Beetles that never moved were excluded from further analyses. Kruskal-Wallis tests were used to test for an effect of radiation source on the behavioural parameters: movement activity, movement speed, angular dispersion of turning angles, pause length and pausing frequency. A multiple comparison post hoc test with

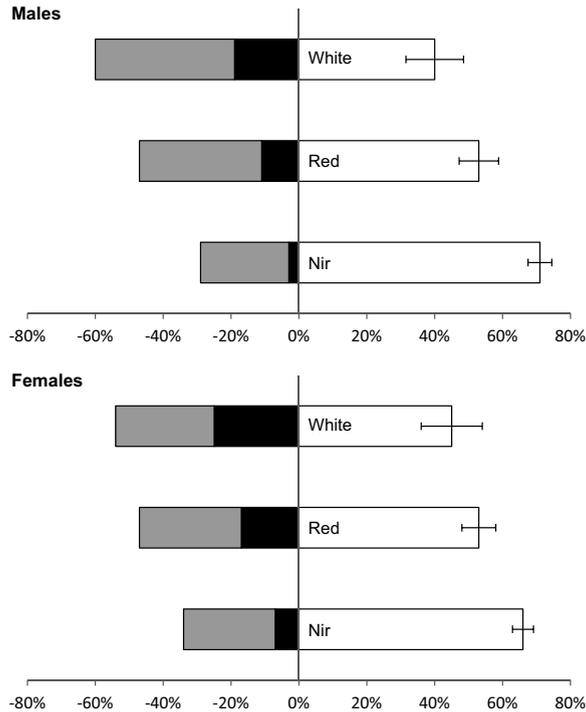


Fig. 2 Time budget of male and female beetles under the different radiation sources. Percentage of time that beetles were visible and not walking (grey) or not visible and assumed to be hiding in the soil (black) are shown on the left side with negative values. Percentage of time that beetles were visible and walking (white) is shown on the right side with positive values. The se are only shown for the percentage of time that beetles were visible and walking.

Bonferroni correction was used to test for significant contrasts between radiation sources. The tests were performed separately for males and females using Matlab R2009a (The MathWorks). Significance was assessed at the 95% confidence level unless otherwise mentioned.

3 Results

3.1 Time budget

The proportion of beetles that moved during the recording period of 240 min was significantly lower in white (74%, $N = 23$) compared to red (98%, $N = 46$) or nir (98%, $N = 42$) (Fisher's exact test: $p = 0.009$ for white-red, $p = 0.011$ for white-nir). There was no significant difference between red and nir (Fisher's exact test: $p \approx 1$).

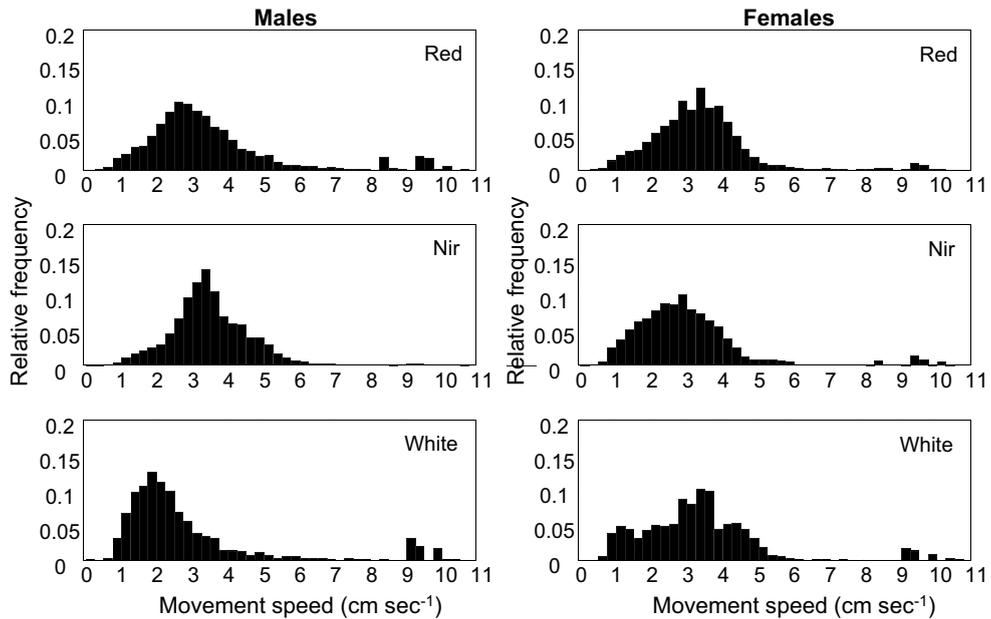


Fig. 3 Relative frequency distribution of movement speed under red, nir and white radiation. Left panels are for males, right panels for females

On average, beetles spent 20.0 min (8.3%; median: 13.8 min) of the 240 min recording period in the arena's interior. During this time they were not visible for 3.6 min on average (18% of time in interior; median 0.2 min). The mean values for the time budget and the behavioural parameters, and the result of the statistical tests are listed in Table 1.

Radiation did not affect the time that males or females spent in the arena's interior nor did it affect the percentage time during which beetles were not visible and assumed to be hiding in the soil (Table 1, Fig. 2). Movement activity, measured as the percentage time spent walking, was significantly affected by radiation in males and marginally significant ($p < 0.1$) in females. Male and female beetles were less active in white than in nir and had intermediate values in red (Table 1, Fig. 2). The percentage of time that beetles were not walking and assumed to be hiding in the soil was not affected by radiation in either gender (Table 1).

3.2 Movement speed and angular dispersion

Radiation significantly affected movement speed of females, but not of males. Females moved on average significantly faster in red and white than in nir (Table 1). The relative frequency distributions of movement speed are shown in Fig. 3.

Table 1 Time budget and behavioural parameters for male (A) and female (B) beetles (mean±se). In the last two columns the test statistic and significance level of the Kruskal-Wallis test for a main effect of radiation is shown. Different letters per behavioural parameter indicate significant differences between treatment means ($p < 0.05$).

A) Males	white	red	nir	χ^2_2	p
Time in arena's interior (min)	26.2±7.2	20.7±3.7	18.5±6.8	2.70	0.26
Not visible (%) ^{1), 2)}	19±9	11±5	3±1	1.84	0.40
Walking (%) ²⁾	40±8 a	53±6 ab	71±3 b	8.11	0.017
Not walking (%) ²⁾	41±7	36±5	26±4	2.57	0.28
Time visible and walking (min)	7.5±1.9	8.5±1.4	14.8±6.4	-	-
Movement speed (cm s ⁻¹) ³⁾	3.5±0.4	3.6±0.2	3.6±0.1	1.8	0.41
Angular dispersion (-) ⁴⁾	0.896±0.023	0.933±0.008	0.923±0.005	5.18	0.075
Time visible and not walking (min)	10.0±4.8	8.3±3.1	3.3±0.6	-	-
Pause length (s) ⁵⁾	10.7±2.8 b	8.5±2.3 ab	4.5±0.7 a	7.34	0.026
Pausing frequency (-)	28.9±8.1	41.3±17.5	18.6±4.5	1.49	0.474
B) Femals	white	red	nir	χ^2_2	p
Time in arena's interior (min)	14.9±4.4	16.2±2.4	22.6±2.9	4.14	0.13
Not visible (%) ^{1), 2)}	25±9	17±5	7±2	3.23	0.20
Walking (%) ²⁾	45±9	53±5	66±3	4.71	0.095
Not walking (%) ²⁾	29±3	30±3	27±3	0.39	0.82
Time visible and walking (min)	6.1±2.2	7.2±1.0	14.9±2.2	-	-
Movement speed (cm s ⁻¹) ³⁾	4.0±0.4 b	3.3±0.1 b	2.9±0.1 a	11.85	0.003
Angular dispersion (-) ⁴⁾	0.919±0.015	0.917±0.008	0.891±0.008	5.45	0.066
Time visible and not walking (min)	4.4±1.5	4.9±1.1	5.7±1.1	-	-
Pause length (s) ⁵⁾	6.3±0.9 b	5.3±0.5 ab	4.4±0.6 a	9.08	0.011
Pausing frequency (-)	19.6±7.9	27.3±5.5	48.3±17.1	5.08	0.079

¹⁾ During this time beetles are assumed to be hiding in the soil. ²⁾ Fig. 2. ³⁾ Fig. 3. ⁴⁾ Fig. 4. ⁵⁾ Fig. 5.

Radiation had a marginally significant ($p < 0.1$) effect on angular dispersion of turning angles in both males and females (Table 1). Males moved straighter in red and nir compared to white, while females moved straighter in white and red compared to nir. The relative frequency distribution of turning angles is shown in Fig. 4.

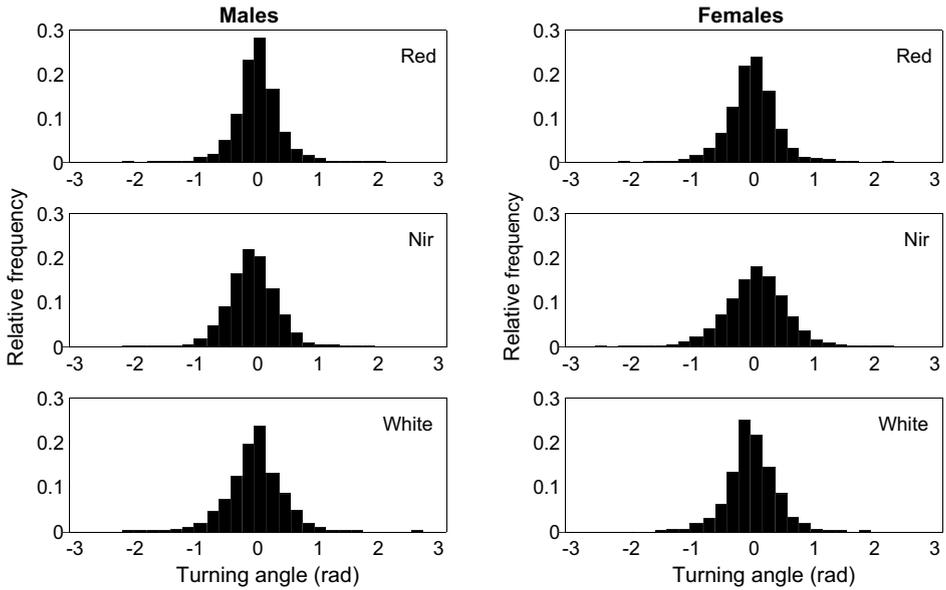


Fig. 4 Relative frequency distribution of turning angles under red, nir and white radiation. Left panel is for males, right for females.

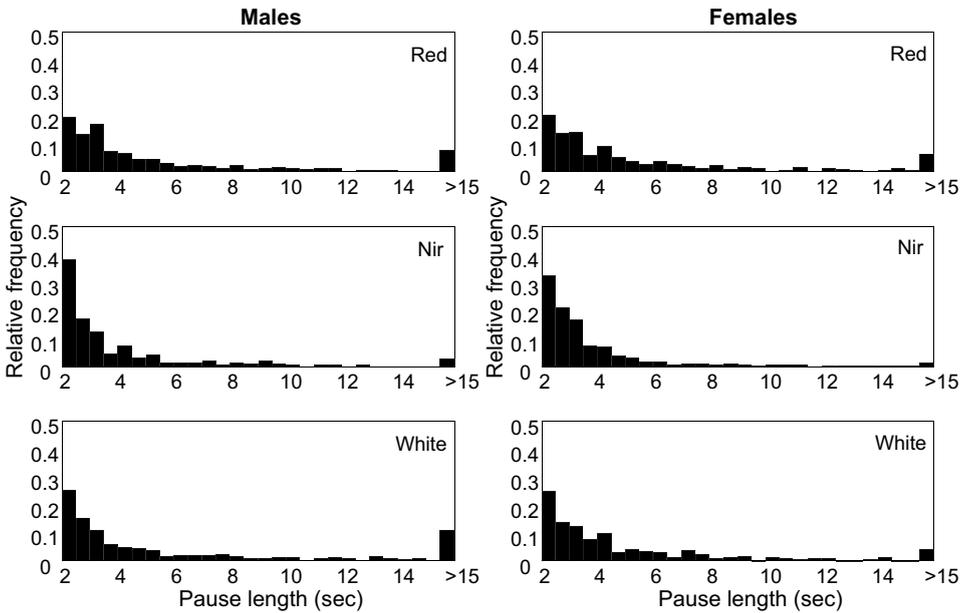


Fig 5 Relative frequency distribution of pause length under red, nir and white radiation. Left panel is for males, right for females.

3.3 Pause length and pausing frequency

Radiation source significantly affected pause length in males and females. Males and females had longer pauses in white than in nir. Pause length in red was intermediate and not significantly different from white or nir (Table 1). The relative frequency distributions of pause length are shown in Fig. 5. Pausing frequency was not significantly affected by radiation in males and was marginally significant ($p < 0.1$) in females (Table 1).

4 Discussion

Evidence collected in this study shows differences in movement behaviour of *P. melanarius* under different sources of radiation. Female beetles were more responsive to radiation source than males, but both genders showed a reduced activity in white compared to nir with intermediate values in red. The reduced movement activity in white was mainly due to longer pauses and a higher percentage of time hiding in white light and for females also due to a higher frequency of pausing (Table 1).

In all treatments beetles made more or less straight crossings from one side of the arena to the other resulting in a small angular dispersion (large mean vector lengths). A straight walk indicates unfavourable conditions from which a beetle wants to escape (Baars 1979). In females, these runs were faster in red and white light than in nir which might indicate that for those beetles conditions were more unfavourable in white and red than in nir. In male beetles movement speed was not affected by radiation and was similar to the speed of females in red and white light.

A potentially confounding factor in this study was the difference in energy density emitted by the radiation sources. The white light source had a net radiant flux of 12 W m^{-2} at ground level, while the radiant flux for the red and nir radiation sources were negligible ($< 0.1 \text{ W m}^{-2}$). While we observed an increase in movement speed of females in white light, this effect was also present for red light for which the emitted radiation was negligible. This suggests that it was the visible part of the electromagnetic spectrum that caused a behavioural change under white and red light rather than heat radiation emitted in the white.

For the majority of behavioural parameters the effect of red was intermediate between effects of white and effects of nir. Variation among individual beetles precludes conclusions on statistically significant differences from white and nir, except for female movement speed.

Variation in behaviour between individuals is a well-known complicating factor in behavioural studies on carabids. Mols (1993) reported large differences in activity among individual *Poecilus versicolor* and related these differences to egg load in female beetles. Other factors that strongly determined movement activity were gut-filling and temperature (Mols 1993). These factors were standardized in this study. There remains large intrinsic variation at the individual level, which is not readily explained by external factors. Larger sample sizes than used in our experiment are needed to ascertain significance of different effects between red and nir. Nevertheless, our results show that red light causes *P. melanarius* to behave in a way that cannot be distinguished from white light.

Movement behaviour is commonly visualized and analysed by the relative frequency distributions of movement parameters (Turchin, 1998). Visual inspection of the relative frequency distributions of movement speed and pause length (Figs 3 and 5) suggests that the distributions under red are different from those under nir. Statistical significance of these differences might be ascertained by the two-sample Kolmogorov-Smirnov (K-S) test (e.g. Vinatier et al., 2010; Hein et al. 2003; Browman et al. 1994). Application of the K-S test on our data confirms that the distributions are indeed significantly different (results not shown). This test, however, is not appropriate for data representing multiple moves by the same individual as independence of samples cannot be assumed. We therefore aggregated the data per individual beetle and resorted to the Kruskal-Wallis test, which has much lower discriminatory power than the K-S test.

Red light is commonly used in studies on the behaviour of nocturnal insects (Ottesen 1990; Heise 1992; Gibson 1995; Depickère et al. 2004; Guy et al. 2008), despite the growing evidence of red light sensitivity in several taxa (e.g. Briscoe and Chittka 2001). Here we demonstrated that movement behaviour of *P. melanarius* is sensitive to the type of radiation source used for observation. For the simulation of total darkness, a nir radiation source thus seems most appropriate. However, in the field total darkness is rare both because of natural light sources such as the moon and stars, but increasingly also due to ecological light pollution (Longcore and Rich 2004). Therefore red light may still be of use for observing ecologically and practically relevant natural night time behaviour.

Acknowledgements

We thank Dine Volker for technical support and two anonymous reviewers for their useful contribution. This project was financially supported by strategic research funds of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation, and co-financed by the DLO Research Programme for LNV, subtheme: Sustainable development and adaptation of ecosystems and landscapes in a metropolitan context (KB-01-008-024-ALT).

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Chapter 3

Quantification of movement of carabid beetles in farmland

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Joop van Lenteren and Walter Rossing

Abstract

Carabid beetles (Coleoptera: Carabidae) are important providers of ecosystem services in farmland by predated on slugs, insect pests and weed seeds. Movement of these beetles between habitats through the season affects their ecological functioning. Here we use meta-analysis of literature data to identify key factors affecting the rate of movement of carabids. Approximating formulas are given to calculate motility μ ($L^2 T^{-1}$), a measure for diffusion of a population in space and time, from literature data on linear displacement distances. A field experiment is conducted to measure movement of the carabid *Pterostichus melanarius* in a homogeneous habitat, and derive motility by fitting a Fokker-Planck diffusion model using inverse modelling. Bias in estimates of motility from literature data is elucidated using the data from the field experiment as a case study. The meta-analysis showed that motility is three times as high in farmland as compared to forested land. The meta-analysis did not identify consistent differences in motility at the species level, and a grouping of species according to gender or size did not demonstrate a significant gender or size effect. The results presented here provide a basis for calculating time-varying distribution patterns of carabids in farmland and assess their ecological functions.

1 Introduction

Carabids are an abundant group of predators in farmland and an important component of the beneficial fauna that contributes to biological control of crop pests (Kromp 1999, Sunderland 2002). The role of carabids in reducing pest populations is affected by their dispersal within and across habitats in the landscape. Hence, spatial movement of carabids has drawn considerable interest in the literature (e.g. Baars 1979a, Wallin and Ekblom 1988, Lys and Nentwig 1991, 1992, Charrier et al. 1997) and several attempts have been made to mathematically model dispersal of carabids (Sherratt and Jepson 1993, Firlie et al. 1998, Westerberg et al. 2005, Benjamin et al. 2008).

A common starting point for modelling arthropod movement is the assumption that an individual follows a random walk. The consequences at population level of random walks by individuals can be simulated with a Fokker-Planck diffusion model (Turchin 1998, Ovaskainen 2008). Turchin (1998) calls the rate of population spread "motility" μ ($L^2 T^{-1}$), in contrast to the diffusion coefficient D which he reserves for the classical Fickian diffusion models. A fundamental difference between Fickian and Fokker-Planck diffusion is that the latter allows steep and persistent gradients in density wherever motility varies in space, whereas Fickian diffusion results in evening out of density differences (Turchin, 1998).

Many studies have been conducted to estimate movement of carabids in the field. Thereby, different methods were used to follow individuals in the field, and different parameters were used to characterize movement. Usually, the rate of movement was expressed as distance covered per day ($L T^{-1}$) averaged over a varying time period (e.g. Thiele 1977, Lys and Nentwig 1991, Holland et al. 2004), or distance covered in a single day (e.g. Wallin and Ekblom 1988, Lys and Nentwig 1992). While daily displacement is easy to interpret and understand, it cannot directly be scaled up to movement at larger time scales, because actual movement has an important random component which is not accounted for in a linear movement rate. Random walk theory predicts that dispersal distance increases with the square root of time (Turchin, 1998; Codling et al., 2008). The distance covered by individuals in a population can be characterized by the variance of the distribution of dispersal distances. This variance increases linearly in time in proportion to the value of the motility parameter: $\sigma^2 = 4\mu t$. Motility is better suited to upscale movement than linear distance, but has only occasionally been estimated from data (Drach and Cancela Da Fonseca 1990, Petit and Burel 1993, Thomas et al. 1998, Bommarco and Fagan 2002).

In this study we present an overview of motility estimates for carabids calculated from movement rates reported in literature. We ask whether there are consistent differences in movement between carabid species and between habitats, and we evaluate whether there are effects of the empirical method used to obtain the movement data and the method used to calculate movement rate. Furthermore, we estimate motility from mark-recapture data using inverse modelling. Inverse modelling is a recent development in the analysis of movement (Ovaskainen 2008) that has advantages over regression methods when the movement domain is heterogeneous. The challenge is in this case to identify simultaneously different model parameters from the same data. Here we evaluate the technique of inverse modelling for a mass mark-recapture dataset with *Pterostichus melanarius* for a homogeneous habitat and compare the estimated motility with a simpler method to determine motility.

2 Materials and methods

In this section we first give an overview of the movement data reported in literature used for the meta-analysis, explain how motility was approximated from dispersal distances, and describe the statistical analysis of the movement data. Second, we describe the experimental design of the mark-recapture experiment with *P. melanarius*, the Fokker-Planck diffusion model for analysis of these data, the parameter estimation procedure, the boundary conditions needed for the numerical solution, the model selection that was used to discriminate between model variants, and the statistical analyses of the data and model parameters. Third, we describe the method used to estimate population density from the activity density of the naturally occurring back-ground population and model parameters motility and trapping efficiency.

2.1 Meta-analysis on motility of carabids

2.1.1 Overview movement data

Studies that report experimental field data on movement or diffusion rate of carabids were gathered from a review by Brouwers et al. (2009) and by a literature search on the databases ISI web of Science, Scopus and Google scholar. The last search was conducted January 2013. The literature search yielded 12 useful references for the meta-analysis. Four of these gave a direct estimate on motility including the present study, and are referred to as Analysis Method 'direct'. Eight studies gave a mean linear dispersal rate plus standard error. This rate was either calculated over recaptures made in a single day and will be referred to as

Analysis Method ‘one-day’ or over multiple days and will be referred to as Analysis Method ‘multiple-days’. Studies that reported carabid movement rate without standard error or variance were not included in the meta-analysis because the calculation of motility from linear movement rate requires an estimate of variability (see below). In most cases, carabid movement was studied with individual mark-recapture. Beetles were individually marked and the moment and location of recapture in a grid of pitfall traps was recorded. Some authors used mass mark-recapture and harmonic radar tracking. Mass mark-recapture is similar to individual mark-recapture except that no individual marking takes place and that the distance between release and recapture is recorded only once. In harmonic radar tracking the position of individuals is recorded continuously over time.

The studies that directly estimated motility from movement data used different analytical methods. Drach and Cancela Da Fonseca (1990) and Petit (1994) derived motility from the slope of the dispersal gradient. Thomas et al. (1998) derived motility from the slope of the linear relationship between squared displacement distances and time duration between release and recapture (see eqn 2 below). The direct estimate of motility for this study is described in section 2.2.

2.1.2 Estimating motility from movement rates

The studies that measured movement rate (displacement per unit time) derived this variable by averaging over dispersal distances divided over time:

$$\bar{r} = \frac{1}{n} \sum_{i=1}^n \frac{d_i}{t_i} \quad \text{eqn 1}$$

According to Turchin (1998), motility can be calculated from observed dispersal distances in a mark recapture experiment in an unbounded space, using the formula

$$\mu = \frac{1}{4n} \sum_{i=1}^n \frac{d_i^2}{t_i} \quad \text{eqn 2}$$

Where d_i is the distance (from the point of release) at which the i^{th} individual is found at time t_i and n is the number of beetles. The distances are squared, divided by the associated t and averaged. The parameter μ is time-invariant.

Estimation of μ based on measures for linear displacement involves making assumptions

that could affect the accuracy of the estimate. Suppose an experiment was terminated after 1 day. Then a simple but biased estimated of μ could be calculated using Turchin's formula as:

$$\hat{\mu} \approx \frac{1}{4} \bar{d}^2 \quad \text{in which} \quad \bar{d} = \frac{1}{n} \sum_{i=1}^n d_i \quad \text{eqn 3}$$

This underestimates the true value of μ because of the variability in the distance covered around the mean and the upward curving relationship between μ and \bar{d} (Jensen's inequality). A better estimate of μ is achieved by including the effect of the non-linear relationship between \bar{d} and μ by using the Delta method (Hilborn & Mangel, 1997, p. 58):

$$E(g(d_i)) = g(\bar{d}) + \frac{1}{2} g''(\bar{d}) \text{var}(d_i) \quad \text{eqn 4}$$

Where E denotes the mathematical expectation, g is a non-linear function linking motility and dispersal distance of individual beetles, i.c.

$$\mu_i = g(d_i, t_i) = \frac{1}{4} \frac{d_i^2}{t_i} \quad \text{eqn 5}$$

and g'' is the second derivative of g with respect to d , which is in this case the distance covered. The second derivative of g is

$$g''(d_i, t_i) = \frac{1}{2t_i} \quad \text{eqn 6}$$

At chosen t_i , the Delta method then yields:

$$\hat{\mu} \approx \frac{1}{4} \bar{d}^2 + \frac{1}{4} \text{var}(d) \quad \text{eqn 7}$$

In the dataset that we used in the meta-analysis, some studies reported average distance covered in 1 day \pm se. We calculated μ from these studies, using equation 7. The variance was calculated by squaring the standard error and multiplying with n , the number of beetles.

Some studies reported average distance covered per day over periods from 1 up to 125 days. None of these studies reported how many beetles were collected on each day. The average distance covered per day, calculated over longer time frames than one day, leads to lower estimates of distance per day because of the less than linear increase of dispersal distance with time. The calculation method of μ was included in the analysis as a covariable to determine whether the expected bias in estimated μ was indeed present.

2.1.3 Statistical analysis

We used a linear mixed model and model selection to analyse the data with literature source as a random term. The explanatory variables of the model were: species (number of levels $L = 13$), habitat type ($L = 2$), observation method ($L = 3$) and analysis method ($L = 3$). Values of motility were log transformed to meet the requirement of normality and homoscedasticity. Normality was checked by plotting the ranked residuals versus quantiles of the normal distribution and homoscedasticity was checked by plotting residuals versus predictions (Zuur et al. 2009). Model selection based on Akaike's criterion, corrected for sample size, AICc, was used to rank models with different combinations of the explanatory variables (Bolker 2008). After evaluation of the ranking order of the models, we tried to simplify the model by replacing the factor species by a variable that grouped species according to a size class ($L = 3$) or habitat preference ($L = 2$) and repeated the model selection for these new models. For the model with the lowest AICc a multiple comparison Tukey test was performed to test for significant differences between levels within factors. All analyses were performed using the Statistical Software package R (R Core Team, 2013), and the packages *nlme*, *MuMin*, *multcomp* and *car*. Specifically, we used the function *lme* for linear mixed models (package *nlme*), the function *dredge* for ranking multiple models with AICc (package *MuMin*), the function *glht* (package *multcomp*) for making multiple comparisons, and the function *qqPlot* (package *car*) for checking normality of the residuals.

2.2 Experimental field study to estimate motility using a Fokker-Planck diffusion model

On 26 June 2009, one thousand adults (500 males plus 500 females) of the carabid beetle *Pterostichus melanarius* were released in a 6 m² release area in a 50 x 250 m large winter triticale field (x *Triticosecale* Wittmack.) at experimental farm Droevendaal, Wageningen, The Netherlands. The wheat was under sown with grass-clover. Beetles had been collected in the week before release using pitfall traps and had been stored in a dark room at 4 °C. The marked beetles were kept together in a container and were fed frozen fly maggots (*Lucilia caesar*) to minimize cannibalism. A few days before release, beetles were marked with red

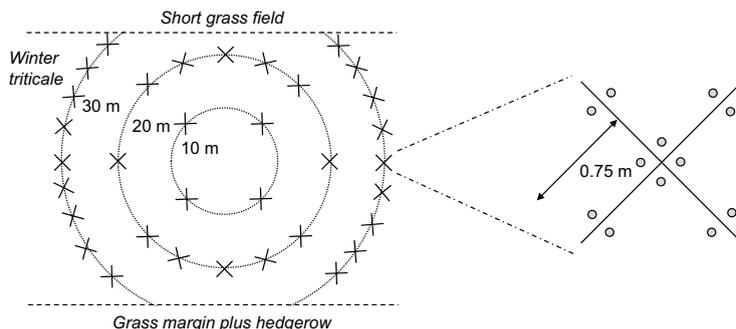


Fig. 1 Schematic overview of the spatial layout of traps in the field experiment. At each trapping station a plastic barrier was placed in a cross shape that contained 3 pitfall traps in each quadrant.

nail polish (HEMA, long lasting nr. 84) (see picture b in the appendix). After release, beetles were recaptured with pitfall traps at distances of 10, 20, 30 m from the centre of the release area (Fig. 1). At each trapping station, a cross-shaped barrier was placed with three pitfall traps in each quadrant (see picture c in the appendix). The numbers of beetles caught per trapping station were counted daily for a period of two weeks. Recaptured beetles were removed from the experiment.

2.2.1 Fokker-Planck diffusion model for spread

Motility was estimated by fitting an extended Fokker-Planck diffusion model to the mark-recapture data:

$$\frac{\partial N_{x,y,t}}{\partial t} = \left(\frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} \right) \mu_{x,y} N_{x,y,t} - (\xi + \alpha_{x,y}) N_{x,y,t} \quad \text{eqn 8}$$

Where $N_{x,y,t}$ is the density of beetles at location (x, y) at time t ; $\mu_{x,y}$ is motility ($\text{m}^2 \text{d}^{-1}$) at location (x, y) ; ξ (d^{-1}) is a relative loss rate of beetles due to other causes than recapture (e.g. death or mark wear), hereafter: relative loss rate; and $\alpha_{x,y}$ (d^{-1}) describes the rate of recapture at location (x, y) which we assume to be a linear function of density at location (x, y) (Baars 1979b, Turchin and Thoeny 1993). We call $\alpha_{x,y}$ the relative recapture rate and assume that $\alpha_{x,y}$ is proportional to the motility, $\mu_{x,y}$, of the beetles. The relative recapture rate $\alpha_{x,y}$ can be interpreted similar to the relative loss rate ξ with one difference that $\alpha_{x,y}$ is location specific while ξ is not. At locations without traps $\alpha_{x,y} = 0$ otherwise:

$$\alpha_{x,y} = \omega \mu_{x,y} \quad \text{eqn 9}$$

where the constant of proportionality ω (m^{-2}), is the efficiency with which beetles are recaptured, hereafter: trapping efficiency.

2.2.2 Estimation of model parameters from data

Values of model parameters in equation 8 were identified by minimizing the Negative Log-Likelihood (*NLL*) (Bolker 2008):

$$NLL = -\sum_{t,i} \ln(L(Y_{t,i} | f(t,i,P))) \quad \text{eqn 10}$$

Where L is the negative binomial or Poisson likelihood of the data $Y_{t,i}$ given model predictions f at time t and trap location i , based on parameter vector P . Model predictions were obtained by numerical integration of equation 8 using the forward central finite difference method (Press et al. 2007) on a lattice of grid-cells with mesh size $\Delta x = \Delta y = 1$ m. The time step of integration Δt was one third of the value obtained from the Von Neumann criterion (Press et al. 2007):

$$\Delta t \leq \frac{h^2}{4\mu + 0.5(\alpha + \xi)h^2} \quad \text{eqn 11}$$

in which $h^2 = \Delta x \Delta y$. The Differential Evolution algorithm (Storn and Price 1997) was used to minimize the *NLL*.

2.2.3 Boundary conditions of the simulation model

We assumed that, once beetles leave the experimental field, they have a constant return probability, which depends on their residence time in the surrounding landscape. In the simulation model, we represented the surrounding landscape by a 1-m wide boundary strip surrounding the field. This boundary strip had a reflective outer edge. Motility in this boundary strip was estimated along with the other parameters. In this way the model was allowed to “choose” the most appropriate, from reflective to absorbing, or intermediate boundary conditions. When motility in the boundary strip is small compared to motility in the field, the boundary strip acts as a semi-absorbent boundary or “slow-release boundary”, i.e. beetles that leave the field return to the field only in part, and after a long time, on average. If motility in the boundary strip is zero, beetles have a zero return probability, resulting in an absorbent boundary. A ratio of motilities in the boundary strip and in the crop field $\gg 1$ will result in a reflective boundary.

2.2.4 Model selection

The most appropriate boundary conditions and error distribution, and the appropriateness of including a loss term were determined by model selection based on Akaike's information criterion (AIC) (Hilborn and Mangel 1997, Van den Hoeven et al. 2005, Bolker 2008). First, boundary conditions were determined by comparing models with absorbing, reflective or slow-release boundaries, respectively along with the other parameters (models 1-4). The model variant with boundary conditions resulting in the lowest AIC was then used to compare models with a Poisson and a Negative Binomial error distribution, respectively. Finally, the model variant with the lowest AIC was used to compare models with and without relative loss rate to determine the significance of this parameter.

2.2.5 Statistical analysis

A binomial test was used to test for a difference in recapture rate between male and female beetles in the field experiment. A Rayleigh test (Batschelet 1981) was used to test for directionality in dispersal of beetles from the central point of release. The model selection procedure to determine the boundary conditions and error distribution was applied for the combined dataset of males and females. The best fitting model was used to determine the significance of the relative loss rate ξ for males and females separately. Motility and relative loss rate of males and females were compared using the 95%-confidence interval of the estimates determined from a log-likelihood profile. The lower and upper bound of the 95% confidence interval were found as the points at which the difference in negative log-likelihood with the best fitting model equals $\chi_1^2(0.95)/2 = 1.92$ (Hilborn & Mangel 1997, Bolker 2008).

2.3 Estimating population density

The relative recapture rate $\alpha_{x,y}$ (eqn 2) multiplied by the density of beetles and the time duration of trapping determines the number of beetles caught in a given amount of time. The relative recapture rate was estimated using data of the marked beetles. Its value may be used to estimate the density of unmarked beetles, assuming marked and unmarked beetles have the same relative capture rate. The population density of the natural population at a particular trapping station was therefore calculated as:

$$N_{density} = \frac{N_{captured}}{\omega\mu\Delta t} \quad \text{eqn 12}$$

The population density was estimated as the average density per trapping station per day.

3 Results

3.1 Meta-analysis on motility of carabids

The raw data on movement rate used for the meta-analysis is presented in the appendix in Table A1. The ranking of models shows that habitat type was an important explanatory variable. It was selected in each of the best four models, representing together an overall model weight of 91.4% (Table 1). Species, on the contrary, had minimal explanatory importance. The effects of analysis method and observation method were confounded with the effect of habitat type. The model with most support from the data included method of analysis and habitat type as explanatory variables.

Significant treatment effects were further explored using pairwise comparisons with Tukey's honestly significant differences provided the main effect was significant. There was a significant difference in predicted motility between 'hedgerow/forest' and 'arable land' (model 6, $z = 2.7$, $p = 0.007$); with motility 3 times higher in arable land than in hedgerow/forest habitat. For the factor method of analysis a significant difference in predicted motility was found between 'one day' and 'multiple days' (model 6, $z = 2.9$, $p = 0.012$), but no significant differences between the 'one day' and 'direct', or between 'multiple days' and 'direct'. Motility derived from measurements obtained by sensed data after one day was approximately a factor 3 higher than motility derived from measurements obtained over multiple days.

When the information on the observed insects was classified according to gender or size class (10-14, 15-19, 20-24 mm) instead of species, these groups had no value in explaining variation in motility. Only when species were pooled according to habitat association (typical habitat: wood or open field) the data gave support for this factor, with habitat preference

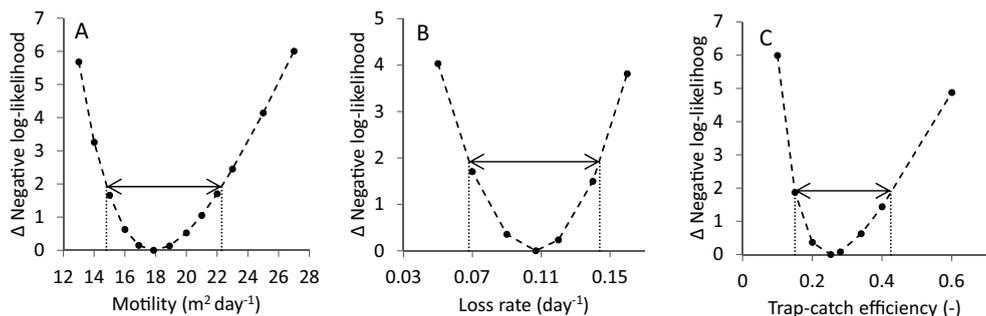


Fig. 2 Likelihood profile for the motility parameter (A), loss rate (B) and trapping efficiency (C) for males and females *P. melanarius* combined (model 1, Table 2). The arrows indicate the 95% confidence interval for the estimated parameter values.

Table 1 Ranking of different parameterizations of a linear mixed effect model that was used to analyse motility in the meta-analysis in relation to the factors: analysis method, observation method, habitat type, and species. Literature source was included all models as a random term. A plus symbol indicates the presence of a factor in the model.

Model	AM	OM	HT	Sp	df	LL	AICc	Δ AICc	Model weight
6	+		+		6	-77.5	168.8	0	0.392
7		+	+		6	-78.2	170.1	1.32	0.202
5			+		4	-80.7	170.1	1.37	0.197
8	+	+	+		8	-76.0	171.1	2.32	0.123
2	+				5	-80.9	173	4.19	0.048
1					3	-84.0	174.4	5.64	0.023
3		+			5	-82.7	176.7	7.91	0.008
4	+	+			7	-80.2	176.9	8.1	0.007
9				+	15	-71.1	184.6	15.84	0
13			+	+	16	-69.3	185	16.25	0
14	+		+	+	18	-65.5	186	17.23	0
15		+	+	+	18	-67.0	189	20.28	0
10	+			+	17	-69.5	189.5	20.76	0
11		+		+	17	-69.6	189.8	21.02	0
16	+	+	+	+	20	-64.4	193.4	24.66	0
12	+	+		+	19	-67.7	195.2	26.45	0

AM: Analysis Method (one day, direct or multiple-days); OM: Observation Method (individual mark-recapture, mass mark-recapture or harmonic radar); HT: Habitat Type (farm land or forested land); Sp: Species.

being included in the best model. This ranking, however, changed when the record for *Carabus nemoralis* with the extremely high motility of $865 \text{ m}^2 \text{ d}^{-1}$ was removed from the data, indicating a rather weak support for habitat preference.

3.2 Estimating model parameters from data using inverse modelling

In total 108 males were recaptured versus 70 females, a significant difference in binomial test at $p = 0.002$. Beetles did not disperse in a preferential direction (Rayleigh test: $r = 0.0673$, $p > 0.05$). A comparison of models with different boundary conditions demonstrated no difference in explanatory power between the models 1-4 (Table 2). The model with reflective boundaries and a negative binomial error distribution (model 1, Table 2) had the

Table 2 Results of model selection using Akaike's Information Criterion (AIC). For the models 1-4 the data on male and female beetles were combined. Models 5-6 is only for male beetles and models 7-8 for females. Parameters in bold were fixed values during the optimization process.

Model	Boundary condition	Error dist.	NLL	AIC	ΔAIC	Model parameters				
						μ_{crop} $m^2 d^{-1}$	ξ d^{-1}	ω m^{-2}	μ_{srb} $m^2 d^{-1}$	k -
1	Reflective	NB	320.2	648.5	0	17.9	0.107	0.253		4.4
2	Absorbing	NB	320.7	649.5	1.0	20.4	0.005	0.164		6.4
3	Reflective	Poisson	321.9	649.9	1.4	17.8	0.096	0.224		
4	Slow-release	NB	319.9	649.9	1.4	17.0	0.114	0.282	295	4.3
5	Reflective	NB	239.0	484.0	0	19.3	0.104	0.286		4.4
6	Reflective	NB	248.4	500.9	16.9	22.5		0.099		4.4
7	Reflective	NB	178.5	0	0	15.5	0.096	0.204		4.4
8	Reflective	NB	183.2	7.4	7.4	17.4		0.080		4.4

μ_{crop} : motility inside the plot; ξ : relative loss rate due to mark wear, mortality and settlement; ω : trapping efficiency; μ_{srb} : motility in the slow-release boundary around the plot; k : dimensionless dispersion parameter of the negative binomial (NB) error distribution.

lowest AIC. A comparison of models with and without a loss term for removal due to recapture demonstrated a lower AIC for the model with loss term for males (model 5, Table 2) and females (model 7, Table 2). The overall motility of the best model (model 1, Table 2) was $17.9 m^2 d^{-1}$ (CI: $14.8-22.3 m^2 d^{-1}$) (Fig. 2A). The overall trapping efficiency was 0.253 (CI: $0.150-0.425$) (Fig. 2B) and the overall loss rate was $0.107 d^{-1}$ (CI: $0.068-0.144 d^{-1}$) (Fig. 2C).

The associated motility estimates for male and females (models 5 and 7, Table 2) were $19.3 m^2 d^{-1}$ (CI: $15.1-25.7 m^2 d^{-1}$) for males and $15.5 m^2 d^{-1}$ (CI: $11.7-21.9 m^2 d^{-1}$) for females. The overlapping confidence interval for the sexes indicate that motility was not significantly different between male and female beetles.

The simulated result of the best model (model 1, Table 2) overestimated cumulative recaptures at 10 m distance during the first week and at 20 m distance at day 5-7, but fell within the 95% confidence margin of the data during the rest of the days (Fig. 3). At 30 m distance, model predictions were within the 95% confidence intervals of the data for all days.

The spatial distribution of beetles over time of the best model (Table 2) is shown in Fig. 4. By day seven, 61% (N = 612) of beetles were lost due to recapture (N = 120), or due to e.g. mortality or mark wear (N = 492). The remaining 388 beetles were more or less homogeneously distributed, albeit still with a slightly higher density in the centre of the plot.

Population densities were calculated using equation 12 with the values for motility and trapping efficiency of the best model ($\omega = 0.253$, $\mu = 17.9 \text{ m}^2 \text{ d}^{-1}$). During the 14 days timespan of the experiment population density varied between (mean \pm se) $1.8 \pm 0.3 \text{ m}^{-2}$ and $9.9 \pm 0.6 \text{ m}^{-2}$.

3.3 Calculating mean daily dispersal distance and motility from data

In this section we show three frequency distributions for different measures of dispersal rate of beetles in the mark-recapture experiment. The first distribution shows the daily displacement distance as it is often calculated in literature (Fig. 5a). The second distribution is for the motility of recaptured beetles (Fig. 5b). And the last distribution is for the dispersal rate calculated from the dispersal distance divided by the square root of time (Fig. 5c). Although, the unit of this variable is $\text{m d}^{-1/2}$ and may not be interpreted as a linear rate, the values nevertheless represent the distance an individual would cover in one day. Double this distance would be covered in 4 days, and three times this distance in 9 days. The frequency distribution of the dispersal distance per square root of time is wider and more towards higher values than the frequency distribution in Fig. 5a. The mean \pm se (N = 178) of the daily displacement distance in Fig. 5a and Fig. 5c are $7.5 \pm 0.3 \text{ m}$ and $3.4 \pm 0.19 \text{ m d}^{-1/2}$, respectively. The motility calculated from the motility of individual beetles is $17.1 \pm 1.3 \text{ m}^2 \text{ d}^{-1}$ (N = 178) and is similar to the motility estimated from the Fokker-Planck model.

There is a clear downward trend in movement rate with increasing duration between release and recapture that approaches an asymptote after two weeks (Fig. 6). For motility the same downward trend is visible, except the peak is at day two. Movement rate determined at the first sampling day was three times higher than movement rate determined over all days.

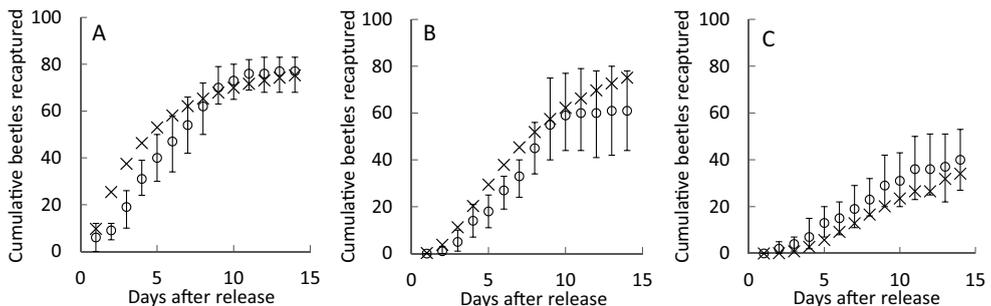


Fig. 3 Cumulative number of observed (\circ) and predicted (\times) *P. melanarius* recaptured over time at 10 (A), 20 (B) and 30 (C) meter distance from the release site in the large field experiment. The predicted values are the result of model 1 (Table 2). The error-bars indicate the 95% CI of the observations.

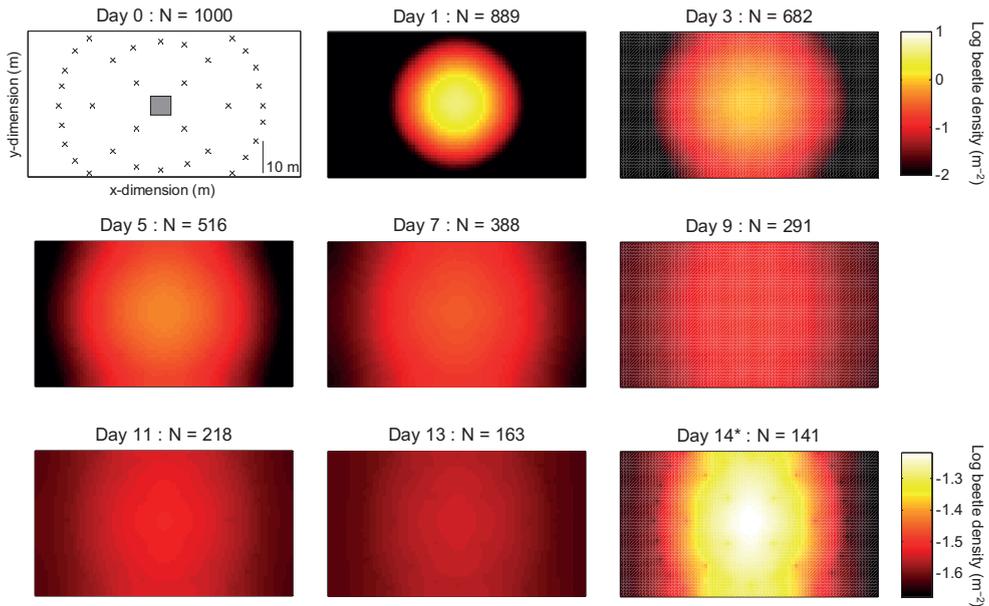


Fig. 4 Time evolution of the distribution of *P. melanarius* in the large field experiment, simulated by model 1 (Table 2). Numbers at the top of the figures are the number of beetles in the simulated space. The figure for day 0 shows the location of trapping stations (x) and the release area (\square). For days 1-13 the colour bar in the top right corner indicates beetle density per 1x1 m grid cell. *For day 14 the colour bar (bottom right corner) is adjusted to express density relative to the maximum density in the plot.

4 Discussion

Analysis of movement data should be consistent with random walk theory to enable scaling up. Calculation of motility satisfies this requirement. In the literature on carabids, movement of carabids has mostly been treated as a linear process in which the estimated movement rate is dependent on the time interval over which it is determined. While reviewing literature on dispersal of carabid beetles we found a large variety of terminology used to describe dispersal rate, including: daily distance covered, minimum distance travelled, mean distance covered, distances moved, distance travelled, and rate of movement. Here we tried to make the available information on movement of carabids comparable by calculating motility from the published data and looked for patterns through meta-analysis.

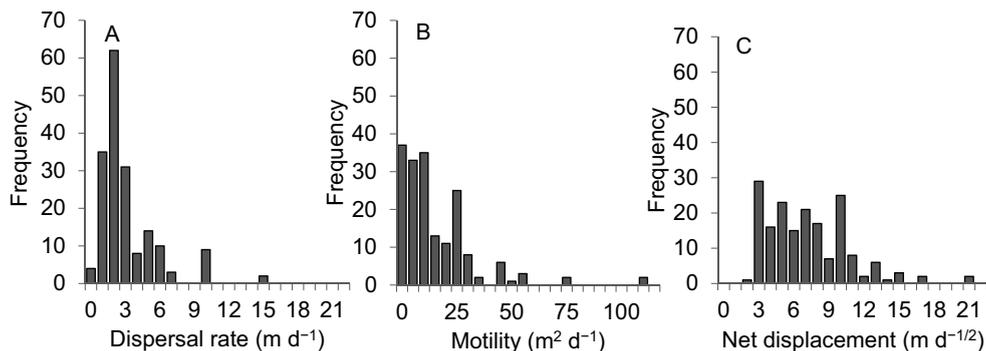


Fig. 5 Three histograms based on the mark-recapture data of the field experiment. (a) Dispersal distances of recaptured individuals divided by time are characterized by a distribution with a short tail and a high frequency of low daily displacement distances. This variable assumes a linear increase of dispersal distance in time, while dispersal distance, as the result of random walk, increases with the square root of time. (b) Motility of recaptured individuals. (c) Net displacement, which gives an accurate prediction of the net distance an individual would cover in one day for $t = 1$.

In the meta-analysis, habitat type, generalized to arable field and forest or hedgerow habitat, was the most important variable explaining differences in motility, while species had no explanatory value. Individual studies, however, show that within habitat types, movement rate can differ between species (Wallin and Ekbohm 1988, Lys and Nentwig 1991, 1992, Wallin and Ekbohm 1994, Holland et al. 2004). From the data available, we cannot confirm that those species effects in individual studies may be generalized across studies. There are two possibilities: either the species differences in individual studies are genuine and general, but the dataset for meta-analysis was too small, and or the data too variable to identify species effects, or – alternatively – the species responses in individual studies are really

different. Both possibilities are plausible. The database is limited, and the variability of motility very large, but it is also likely that species have different movement responses in different studies because, e.g., of interactions with habitat (Greenslade 1964), responses to experimental manipulation (Bommarco and Fagan 2002), or intrinsic motivation to move in relation to feeding state (Mols 1993), etc.

The meta-analysis also showed an effect of the method of calculating movement rate. Movement rate determined after one day was approximately three times higher than movement rate calculated over multiple days. We illustrate the effect of sampling interval on movement rate and motility for our own field data with *P. melanarius*. Movement rate and motility decreased with increasing time window over which these variables were estimated.

As time increases, more slow walking individuals will be captured which lower the average movement rate. This unwanted bias is avoided when motility is calculated directly from the data instead of calculating it from movement rate.

Observation method had little effect on motility. However, the motility estimate derived from harmonic radar tracking tended to be higher than motility derived from mass-mark recapture. In mark-recapture studies the data is always censored and this is likely to result in some negative bias in estimated μ . If, for instance, there are no or few traps at far distance from the point of release, an underestimate of μ should be expected due to under-representation of far dispersal in the sample. Following individuals in the open field, i.e. with harmonic radar, should result in unbiased estimates of μ as the distances from all released individuals are known.

We showed that motility can be calculated from squared displacement distance and the time duration between release and recapture (see eqn 2) and that this estimate was equal to motility estimated from a Fokker-Planck diffusion model calibrated to the same data. In the first case, motility was calculated as an average over motility of individuals, in the second case motility was estimated from a population density distribution fitted to the recapture data. The similarity in motility between these two very different approaches strengthens the confidence in motility as a suitable concept for quantifying dispersal rate of carabid beetles, and in inverse modelling as a method to retrieve movement parameters from observed patterns.

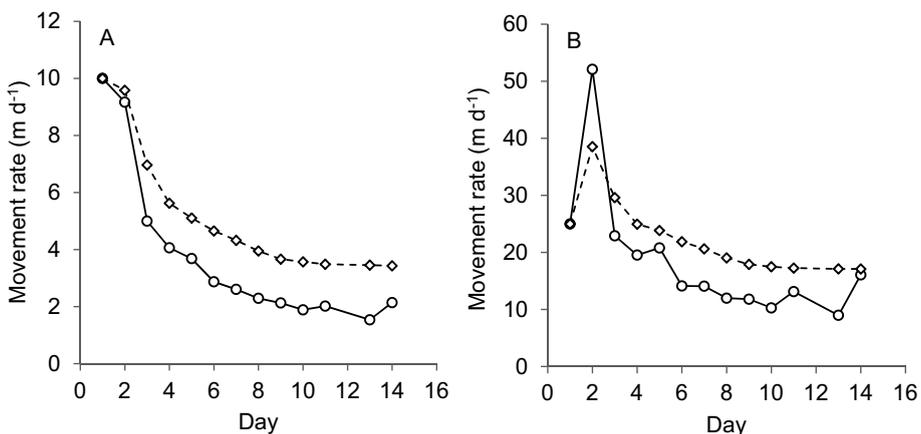


Fig. 6 Movement rate (A) and motility (B) calculated from the field data for each recapture day (solid line and open circles) and cumulated over time (dashed line, open diamond).

From the motility of individual beetles we calculated the net displacement distance as $2\sqrt{\mu}$. The net displacement has the unit $\text{m d}^{-1/2}$ while movement rate calculated as a linear process has the unit m d^{-1} . The net displacement reflects more the true daily displacement distance than dispersal rate calculated as a linear process. In this study the net displacement was $7.5 \text{ m d}^{-1/2}$, while movement rate calculated as a linear process was only 3.4 m d^{-1} . Calculating movement rate as a linear process may thus underestimate the true daily displacement distance by a factor two. The net displacement distance is not dependent on the time interval over which it is calculated and can be used for scaling up movement. *Pterostichus melanarius* for example may cover during a growing season of 14 weeks an average distance of 74 m ($7.5\sqrt{14*7}$), spanning an area of 1.7 ha if we take 74 m as the radius of a circle. This estimate of area covered is close to the lower limit of $2 - 7 \text{ ha}$ predicted by Firle et al. (1998) for this species for the same time period using an individual based simulation model parameterized on tracking data of movement in the field. After 30 days the expected mean dispersal distance of *P. melanarius* is 41 m , which is in accordance with the observation of Thomas et al. (1998) in a large mark-recapture experiment that few individuals dispersed further than 50 m in 30 days. With motility and its' associated true daily dispersal distance we thus can compare results between studies beyond the scale at which the observations were taken.

The next challenge in the study of carabid movement is to incorporate habitat heterogeneity and to study the influence of habitat heterogeneity and habitat interfaces on movement. The foundation for a methodology to analyse mark-recapture data from heterogeneous environment are laid in this study with the evaluation of a Fokker-Planck diffusion model.

Acknowledgements

We thank Dine Volker for technical support during the experiments and thank Herman Berghuijs and Juliette Marsan who contributed to this work as part of their Msc thesis/ internship. This project was financially supported by strategic research funds of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation and was co-funded by the strategic research program "Sustainable spatial development of ecosystems, landscapes, seas and regions" (KB-01-008-024-ALT).

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Appendix

Table A1 Motility of carabid beetles approximated from mean daily displacements reported in literature or directly estimated from data.

Species	Habitat type	Month	Gender	FM	AM	Rate m day ⁻¹	N	σ^2	Motility m ² day ⁻¹	Reference
<i>Pterostichus melanarius</i>	arable matrix	May-July	m	IMR	m	5.5	101	25	14	Holland et al. 2004
<i>Pterostichus madidus</i>	arable matrix	May-July	m	IMR	m	12.0	52	88	58	Holland et al. 2004
<i>Pterostichus madidus</i>	winter wheat	May-July	m	IMR	m	3.1	66	11	5	Holland et al. 2004
<i>Pterostichus melanarius</i>	arable matrix	May-July	f	IMR	m	5.6	96	24	14	Holland et al. 2004
<i>Pterostichus madidus</i>	arable matrix	May-July	f	IMR	m	12.0	52	88	58	Holland et al. 2004
<i>Pterostichus madidus</i>	winter wheat	May-July	f	IMR	m	2.9	5	2	3	Holland et al. 2004
<i>Pterostichus madidus</i>	arable matrix	May-July	m + f	IMR	m	12.0	121	77	55	Holland et al. 2004
<i>Pterostichus madidus</i>	winter wheat	May-July	m + f	IMR	m	4.0	134	34	12	Holland et al. 2004
<i>Pterostichus melanarius</i>	arable matrix	May-July	m + f	IMR	m	5.9	211	34	17	Holland et al. 2004
<i>Harpalus rufipes</i>	potato	July-Aug	m	MMR	m	6.5	9	37	20	Zhang et al. 1997
<i>Harpalus rufipes</i>	oats	July-Aug	m	MMR	m	5.7	29	22	14	Zhang et al. 1997
<i>Carabus nemoralis</i>	arable matrix	April-May	m + f	IMR	m	5.0	15	60	21	Kennedy 1994
<i>Poecilus cupreus</i>	winter wheat	May-July	m	IMR	m	15.1	57	195	106	Lys and Nentwig 1991
<i>Pterostichus anthracinus</i>	winter wheat	May-July	m	IMR	m	7.6	9	31	22	Lys and Nentwig 1991
<i>Pterostichus melanarius</i>	winter wheat	May-July	m	IMR	m	7.4	8	16	18	Lys and Nentwig 1991
<i>Poecilus cupreus</i>	after threshing ^a	July-Aug	m	IMR	m	16.1	5	159	105	Lys and Nentwig 1991
<i>Pterostichus melanarius</i>	after threshing ^a	July-Aug	m	IMR	m	12.1	13	69	54	Lys and Nentwig 1991
<i>Poecilus cupreus</i>	after tillage ^a	Sep	m	IMR	m	12.3	13	125	69	Lys and Nentwig 1991
<i>Pterostichus melanarius</i>	after tillage ^a	Sep	m	IMR	m	12.0	59	119	66	Lys and Nentwig 1991
<i>Harpalus rufipes</i>	after tillage ^a	Sep	m	IMR	m	14.2	3	22	56	Lys and Nentwig 1991

Continuation of Table A1

Species	Habitat type	Month	Gender	FM	AM	Rate m day ⁻¹	N	σ^2	Motility m ² day ⁻¹	Reference
<i>Pterostichus niger</i>	after tillage ^a	Sep		IMR	m	14.9	15	182	101	Lys and Nentwig 1991
<i>Nebria brevicollis</i>	hedgerow+grass	Oct		IMR	m	1.5	83	7	2	Joyce et al 1999
<i>Pterostichus melanarius</i>	cereal		m + f	HR	s	5.3	39	66	24	Wallin and Ekbohm 1988
<i>Pterostichus melanarius</i>	deciduous wood		m + f	HR	s	4.4	20	10	7	Wallin and Ekbohm 1988
<i>Pterostichus niger</i>	cereal		m + f	HR	s	16.3	33	381	162	Wallin and Ekbohm 1988
<i>Pterostichus niger</i>	deciduous wood		m + f	HR	s	10.5	12	131	60	Wallin and Ekbohm 1988
<i>Harpalus rufipes</i>	cereal		m + f	HR	s	7.3	4	9	16	Wallin and Ekbohm 1988
<i>Carabus nemoralis</i>	deciduous wood		m + f	HR	s	5.4	12	24	13	Wallin and Ekbohm 1988
<i>Pterostichus melanarius</i> + <i>Pterostichus madidus</i>	potato	Aug	m + f	MMR	s	9.1	13	28	28	Gordon and McKinlay 1986
<i>Poecilus cupreus</i>	winter wheat	May-June		IMR	s	19.0	61	187	137	Lys and Nentwig 1992
<i>Pterostichus anthracinus</i>	winter wheat	May-June		IMR	s	14.7	18	94	78	Lys and Nentwig 1992
<i>Carabus granulatus</i>	winter wheat	May-June		IMR	s	28.6	7	220	259	Lys and Nentwig 1992
<i>Pterostichus melanarius</i>	winter wheat	May-June		IMR	s	16.1	5	171	107	Lys and Nentwig 1992
<i>Pterostichus niger</i>	winter wheat	May-June		IMR	s	11.1	2	52	44	Lys and Nentwig 1992
<i>Harpalus rufipes</i>	winter wheat	May-June		IMR	s	23.9	2	9	145	Lys and Nentwig 1992
<i>Poecilus cupreus</i>	winter wheat	May-July		IMR	s	16.5	139	145	104	Lys and Nentwig 1992
<i>Pterostichus anthracinus</i>	winter wheat	May-July		IMR	s	11.9	10	55	49	Lys and Nentwig 1992
<i>Carabus granulatus</i>	winter wheat	May-July		IMR	s	32.0	4	366	347	Lys and Nentwig 1992
<i>Pterostichus melanarius</i>	winter wheat	May-July		IMR	s	18.1	31	283	152	Lys and Nentwig 1992

Continuation of Table A1.

Species	Habitat type	Month	Gender	FM	AM	Rate m day ⁻¹	N	σ^2	Motility m ² day ⁻¹	Reference
<i>Poecilus cupreus</i>	after harvest ^a	Aug-Sep		IMR	s	7.7	3	9	17	Lys and Nentwig 1992
<i>Pterostichus anthracinus</i>	after harvest ^a	Aug-Sep		IMR	s	8.6	6	35	27	Lys and Nentwig 1992
<i>Carabus granulatus</i>	after harvest ^a	Aug-Sep		IMR	s	17.1	7	129	105	Lys and Nentwig 1992
<i>Pterostichus melanarius</i>	after harvest ^a	Aug-Sep		IMR	s	13.3	106	117	74	Lys and Nentwig 1992
<i>Pterostichus niger</i>	after harvest ^a	Aug-Sep		IMR	s	15.3	14	141	94	Lys and Nentwig 1992
<i>Harpalus rufipes</i>	after harvest ^a	Aug-Sep		IMR	s	34.9	6	87	326	Lys and Nentwig 1992
<i>Carabus nemoralis</i>	arable matrix	April-May		HR	s	55.2	14	417	865	Kennedy 1994 ^b
<i>Abax ater</i>	beech wood	June-Nov		IMR	d		50		7	DCF 1990 ^c
<i>Orinocarabus nemoralis</i>	beech wood	June-Nov		IMR	d		8		46	DCF 1990 ^c
<i>Procrustes purpurascens</i>	beech wood	June-Nov		IMR	d		11		71	DCF 1990 ^c
<i>Abax ater</i>	woodland			IMR	d		85		5	Petit 1994 ^a
<i>Abax ater</i>	hedgerow			IMR	d		62		20	Petit 1994 ^a
<i>Pterostichus melanarius</i>	winter barley	June-Aug	m	IMR	d		750		28	Thomas et al. 1998
<i>Pterostichus melanarius</i>	winter barley	June-Aug	f	IMR	d		485		24	Thomas et al. 1998
<i>Pterostichus melanarius</i>	winter triticales	June-July	m	MMR	d		108		19	This study
<i>Pterostichus melanarius</i>	winter triticales	June-July	f	MMR	d		70		16	This study

FM: Field Method (HR 'Harmonic radar'; MMR: 'Mass mark-recapture'; IMR: 'individual mark-recapture'; AM: Analysis Method (m 'multiple-days', s 'one-day', d 'direct').

^a winter wheat

^b Kennedy (1994) reports a standard error of 20.4 which corresponds to an unrealistic large variance of 5832. We interpreted the value mentioned in the paper: therefore as the standard deviation and used this to determine the variance in the table.

^c Drach and Cancela da Fonseca 1990; Motility was expressed in m² week⁻¹ and divided by 7 to get m² d⁻¹.

Chapter 4

Understanding distribution patterns of an arthropod ground predator across two habitats based on within and between habitat movement characteristics

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Abstract

Insect distribution patterns in agro-landscapes are the outcome of movement within habitats and across habitat interfaces. Little is known about the relative importance of the two processes. We monitored the distribution pattern of the generalist predator *Pterostichus melanarius* between adjacent fields of oilseed radish and rye in a mark-recapture experiment. Model selection was used to assess the support in the data for distinguishing behaviour at the habitat interface. The field study was supported by a study of movement behaviour in 5 m² experimental arenas using a high resolution automatic video recording system. Movement in the field was satisfactorily described by a Fokker-Planck diffusion model with equal motility (i.e. diffusion rate) in the two crops, and preference for oilseed radish over rye at the interface between the two crops. Beetles moved 1.5 times more frequently from rye into oilseed radish than vice versa. Analysis of video tracking data resulted in estimates of motility that, when scaled up were close to those obtained in the field. The arena data indicated greater frequency of habitat entry into oilseed radish as compared to rye. Thus, the studies at the smaller and larger scales gave qualitatively and quantitatively similar results. The approach provides a framework for evaluation of movement within and across habitats as a basis for understanding distribution patterns in landscape mosaics.

1 Introduction

Movement between habitats determines patterns of pest and beneficial arthropod species in agricultural landscapes (Landis and Marino 1999). Because movement of arthropods is difficult to measure directly, empirical research has focused on patterns of population density (e.g. Holland et al. 2005) while simulation modelling has been used to evaluate consequences of alternative assumptions on movement for pattern formation in particular landscape settings (e.g. Johnson et al. 1992, Tischendorf et al. 1998, Söndgerath and Schröder 2002, Jopp and Reuter 2005, Westerberg et al. 2005, Benjamin et al. 2008). Model studies are useful to generate hypotheses on the processes that generate patterns of population density but need to be confronted with data to test their validity.

The confrontation of models with data is a recent development in the field of spatial ecology (Ovaskainen 2008, Xiao et al. 2012). It has predominantly addressed habitat specialists moving between their preferred (or host) habitat and the surrounding (hostile) matrix. Reeve et al. (2008), for example, quantified the response of leaf hoppers to the interface between its host habitat and the surrounding matrix. They found higher diffusion rates in the matrix and at the interface a strong bias of movement towards the host habitat. Also for butterfly species moving in a heterogeneous landscape behaviour at habitat interfaces was an important attribute determining population densities in host patches (Schtickzelle and Baguette 2003, Ovaskainen 2004). The attraction of habitat specialists to host patches is not surprising. However, for a large group of organisms that have a less distinct habitat preference, including many carabid species, it is unclear how species respond to habitat interfaces.

Carabid beetles are important predators of arthropod pests and weed seeds in agroecosystems (e.g. Sunderland 2002, Westerman et al. 2003) and landscape manipulation has been proposed as a means to enhance their role in pest suppression and reduce pesticide use (Landis et al. 2000). Many carabid species are opportunistic feeders, scavenging through the landscape in search for food (Lövei and Sunderland 1996). Net population displacement from one habitat to the other (Duelli et al. 1990, Thomas et al. 2006) could be the result of differences in habitat specific motility (i.e. diffusion rate, see Chapter 3) of beetles or effects on motility by habitat interfaces (Bommarco and Fagan 2002). Habitat specific motility includes processes that affect movement behaviour within habitats, causing a net flux of beetles from a habitat with high motility to a habitat with low motility. Habitat specific motility may be affected by the response of animals to habitat quality (Kareiva 1982) or vegetation structure (Crist et al. 1992). Habitat interfaces may cause organisms to bias

their movement towards or away from the interface (Ovaskainen and Cornell 2003). Discriminating between the habitat specific differences in behaviour and interface mediated behaviour is not straightforward as both mechanisms may generate the same pattern of population spread. Bommarco and Fagan (2002) for example, found a model with edge behaviour to give a better description of the data than a model without edge behaviour, but did not test whether the extra parameters needed to simulate edge behaviour were actually supported by the data.

The objective of this study is to improve our understanding of the dispersal ecology of carabids in an agricultural landscape. For this purpose we postulate a series of models that represent assumptions about the processes underlying dispersal across habitats and use Akaike's Information Criterion (AIC) to select the model that receives most support from data. As experimental model system we use the generalist carabid predator *Pterostichus melanarius* in two adjacent habitats: crops of oilseed radish (*Raphanus sativus*) and rye (*Secale cereale*). *Pterostichus melanarius* movement was studied in a mark-recapture experiment at the field scale and by video tracking of beetles in experimental arenas. While the mark-recapture experiments captured the spatial patterns resulting from beetle movement, video tracking of beetles at a smaller spatial scale allowed more detailed insight into the underlying movement behaviour.

2 Methods

2.1 Field experiment

Dispersal of adult females of *P. melanarius* was measured in 2009 in a field of 229 x 52m at the organic farm Droevendaal in Wageningen, the Netherlands. On half of the field oilseed radish (*Raphanus sativus*; var. Brutus) was grown, on the other half rye (*Secale cereale*; var. Admiraal) (see picture d in the appendix). Both crops were sown in the first week of August 2009. The virtual line between the adjacent rows of oilseed radish and rye was taken to be the habitat interface. The field was surrounded by a 3-6m wide grass margin, which on the north side included 1.5-2.5m tall shrubs and trees.

Female adult beetles for release in the field experiments were collected from a grass/clover field in the weeks preceding the experiment using pitfall traps. Beetles were stored in containers (45x30x15cm; about 200 beetles per container) on a substrate of moist potting soil in a dark room at 4°C and fed frozen fly maggots (*Lucilia caesar*). A few days before

release, the beetles were marked with a dot of nail polish on the elytra. Pink/golden nail polish (OPI Nail lacquer NL B777/H41) was used for beetles released in oilseed radish/rye.

Releases were made at 6 p.m. on 7 September 2009 in two lines parallel to and 10m removed from the interface (Fig. 1). In both oilseed radish and rye 1015 beetles were released. Recaptures were made in pitfall traps placed in lines at 10, 20, and 30m at either side of the release lines. Pitfall traps had a diameter of 8.5cm and were arranged in 4 trapping stations per line with two traps per station at 50cm distance from each other, and 140cm between

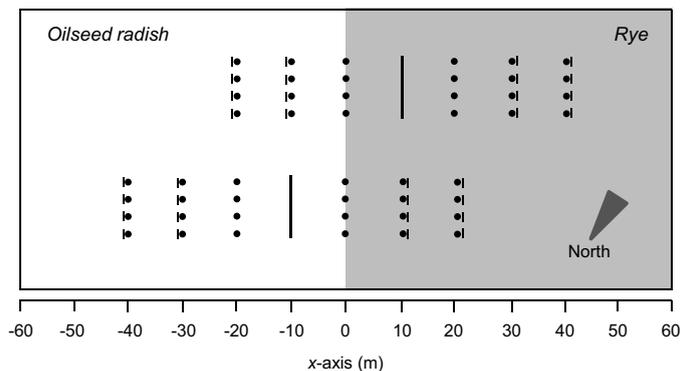


Fig. 1. Spatial layout of the field experiment at Droevendaal organic experimental farm in Wageningen, the Netherlands. *Pterostichus melanarius* were released at the long vertical lines and recaptured at trapping stations with (|•, •|) or without (•) screens.

stations. Pitfall traps at 20 and 30m from the release line were equipped with screens to enhance trapping, while traps at 10m from the release line were not equipped with screens in order to minimize interference with dispersal (Fig. 1). Traps were sampled at 1, 2 or 3 day intervals over a period of 23 days, until 30 September 2009. Recaptured beetles were removed from the experiment. Results were pooled per trapping station.

2.1.1 Analysis of mark-recapture data

We used model selection to determine whether behaviour at the habitat interface was needed to describe dispersal of carabid beetles between adjacent crop habitats. Thus, a suite of candidate models is fitted to data with maximum likelihood, and an information criterion is used to weigh goodness of fit against the number of parameters of a model, penalizing models that require many parameters to “explain” the data (Hilborn and Mangel 1997, Bolker 2008). We defined different versions of a Fokker-Planck diffusion model with

preferential movement at the habitat interface to simulate carabid dispersal. The model contains terms accounting for (1) random movement, including interface-mediated behaviour, (2) beetles lost by trapping, and (3) beetles lost due to mortality and mark wear:

$$\frac{\partial N(x, y, t)}{\partial t} = \nabla^2 [\mu(x, y) N(x, y, t)] - \alpha(x, y) N(x, y, t) - \xi N(x, y, t) \quad \text{eqn 1}$$

In this equation ∇^2 is the Laplace operator that takes the second derivative in the x and y direction, $\mu(x, y)$ is the motility ($\text{m}^2 \text{d}^{-1}$), which determines the rate of random movement and can vary spatially according to the local conditions (e.g. the crop). $N(x, y, t)$ is beetle density (m^{-2}) at location (x, y) and time (t) , $\alpha(x, y)$ is the relative rate of beetle removal by traps, which

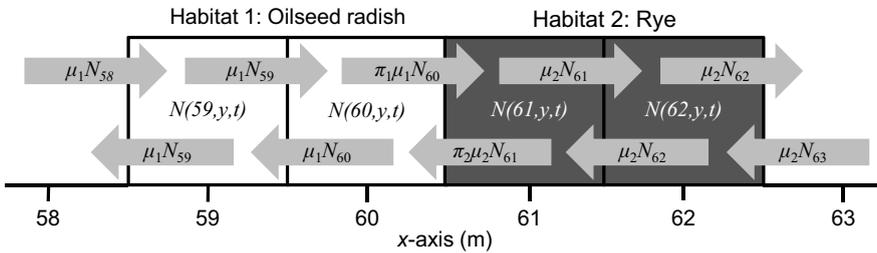


Fig. 2. Representation of fluxes in the x -direction in the spatial simulation model. $N(x, y, t)$ is the density of beetles (m^{-2}) in a grid cell with coordinates (x, y) at time t . μ_1 and μ_2 ($\text{m}^2 \text{d}^{-1}$) are the motilities of beetles in oilseed radish and rye, respectively. π_1 and π_2 are dimensionless and modify the fluxes of beetles between the two habitats.

varies depending upon presence/absence of a trap (hereafter: relative capture rate; d^{-1}), and ξ is the relative loss rate of marked beetles due to death or mark wear (hereafter: relative loss rate; d^{-1}). Just left and right from the interface, $\mu(x, y)$ was multiplied by a flux-modifier (π_1 and π_2 , respectively) to simulate interface behaviour (Fig. 2). Equation 1 was solved numerically using the forward central finite difference method on a lattice of grid cells (Press *et al.*, 2007) with mesh size $\Delta x = \Delta y = 1$ m. The change in density of beetles in a grid cell centred on coordinates (x, y) during a time step Δt was calculated as:

$$\Delta N(x, y, t) = (I_x + I_y - (\xi + \alpha(x, y)) N(x, y, t)) \Delta t \quad \text{eqn 2}$$

where I_x and I_y represent the net rate of change of beetle density in a grid cell due to fluxes over the border with adjacent cells in the x and y directions, respectively. The flux of beetles in the x -direction and y -direction are shown in equation 4 and 3, respectively. An adjusted

form of the system of equation 4 (x-direction) was used for cells bordering the interface between oilseed radish and rye at $i = 60.5$ m (Fig. 2) to allow for preference of beetles for one habitat over the other when at the interface (eqn 5).

$$I_y = \begin{cases} \left(\frac{\mu_1 N(x, y-1, t) - 2\mu_1 N(x, y, t) + \mu_1 N(x, y+1, t)}{\Delta y^2} \right) & x \text{ element of } \{0, 1, \dots, 60\} \\ \left(\frac{\mu_2 N(x, y-1, t) - 2\mu_2 N(x, y, t) + \mu_2 N(x, y+1, t)}{\Delta y^2} \right) & x \text{ element of } \{61, 62, \dots, 120\} \end{cases} \quad \text{eqn 3}$$

$$I_x = \begin{cases} \left(\frac{\mu_1 N(x-1, y, t) - 2\mu_1 N(x, y, t) + \mu_1 N(x+1, y, t)}{\Delta x^2} \right) & x \text{ element of } \{0, 1, \dots, 59\} \\ \left(\frac{\mu_2 N(x-1, y, t) - 2\mu_2 N(x, y, t) + \mu_2 N(x+1, y, t)}{\Delta x^2} \right) & x \text{ element of } \{62, 63, \dots, 120\} \end{cases} \quad \text{eqn 4}$$

$$I_x = \begin{cases} \left(\frac{\mu_1 N(x-1, y, t) - \mu_1 N(x, y, t) - \pi_1 \mu_1 N(x, y, t) + \pi_2 \mu_2 N(x+1, y, t)}{\Delta x^2} \right) & x = 60 \\ \left(\frac{\pi_1 \mu_1 N(x-1, y, t) - \pi_2 \mu_2 N(x, y, t) - \mu_2 N(x, y, t) + \mu_2 N(x+1, y, t)}{\Delta x^2} \right) & x = 61 \end{cases} \quad \text{eqn 5}$$

Here, μ_1 is motility in oilseed radish, and μ_2 motility in rye. The dimensionless flux-modifier π_1 affects the flux of beetles from oilseed radish to rye, while π_2 modifies the opposite flux (Fig. 2). The meaning of these flux-modifiers can be understood by considering a beetle that is situated exactly on the interface. Its probability of moving to rye is $\pi_1/(\pi_1+\pi_2)$ while its probability of moving to oilseed radish is $\pi_2/(\pi_1+\pi_2)$. When $\pi_1 > \pi_2$ (or $\pi_1 < \pi_2$) the direction of movement on the interface is biased towards rye (or oilseed radish). For $\pi_1 = \pi_2 = 1$, movement over the interface is entirely determined by the habitat-specific motilities and densities (see Fig. 2). When $\pi_1 = \pi_2 > 1$ (or $\pi_1 = \pi_2 < 1$), both fluxes are increased (or decreased), but there is no bias in the behaviour at the interface. This presents an interface that is easy (difficult) to cross, e.g. a barrier. While the relative sizes of the π 's determine the bias, their absolute sizes determine the size of the fluxes over the interface, and hence the speed at which the population crosses the interface.

Relative capture rate $\alpha(x, y)$ is a linear function of μ according to:

$$\alpha(x, y) = \begin{cases} \omega_i \mu_j & i = 0, 1 \text{ at trapping locations without or with trapping screen} \\ 0 & \text{all other locations} \end{cases} \quad \text{eqn 6}$$

where the constant of proportionality ω_i (m^{-2}) is the efficiency with which beetles are recaptured at a trapping station with ($i = 1$) or without ($i = 0$) a screen. The index j identifies the habitat to which the motility parameter applies. The parameter fitted is ω_i , not α .

The simulated field of grid cells was bordered on all sides by a 1-m wide “slow-release” boundary with a reflective outer edge. This slow-release boundary represents in a crude way the “landscape context” of the experiment. The motility μ_0 in this slow-release boundary determines how long beetles are retained before returning to the field. The time step of integration Δt used in solving the model (eqn 2) was one third of the upper value Δt_{\max} obtained from the Von Neumann criterion (Press et al. 2007):

$$\Delta t_{\max} \leq \frac{h^2}{4\mu_{\max} + 0.5(\alpha_{\max} + \xi)h^2} \quad \text{eqn 7}$$

in which $h^2 = \Delta x \Delta y$, and μ_{\max} and α_{\max} are the maximum values used in model calibration.

2.1.2 Model calibration and model selection

Variants of the model described by equation 2 were calibrated to the data by minimizing the negative log-likelihood:

$$NLL = -\sum_{t,i} \ln(L(Y_{t,i} | f(t,i,P)))$$

where L is the negative binomial likelihood of the data $Y_{t,i}$, given model predictions f at time t and trap location i , based on parameter vector P . The NLL was minimized using a differential evolution algorithm (Storn and Price 1997), implemented in C++ code that is part of the COMPASS framework (Groot et al. 2012).

The value of motility in the slow-release boundary μ_0 and the dispersion parameter of the negative binomial error distribution k were estimated once by calibrating the model (parameterized as model 4 in Table 1) to the data. The calibrated values for μ_0 and k were set as constants during the calibration of the model variants.

The most complex model for beetle dispersal contained seven parameters (μ_1 , μ_2 , ξ , ω_0 , ω_1 , π_1 , π_2). We fitted 16 alternative models to the data, and used Akaike’s information criterion (AIC) to rank these models according to the level of support from the data (Hilborn and

Mangel 1997, Bolker 2008). AIC was calculated as $AIC = 2 NLL + 2n$, where NLL is the negative log likelihood, a measure for goodness of fit, and n is the number of parameters. ΔAIC was calculated by comparing a model's AIC to the minimum AIC of the best model. Models that differ less than 2 AIC units have similar support from the data.

2.2 Arena experiments

2.2.1 Experimental setting

Beetle movement was recorded in autumn 2009 in two arenas of 2 x 2.5m with either oilseed radish (*Raphanus sativus* var. Brutus) or winter rye (*Secale cereale* var. Admiraal), in a climate controlled greenhouse (see picture e in the appendix). The arenas were filled with 5cm moist sandy soil collected from the Droevendaal organic experimental farm, on top of 5cm of potting soil. Similar to agronomic practice the species were sown at 12.5cm row distance and a sowing density of 30 kg ha⁻¹ for oilseed radish and 100 kg ha⁻¹ for rye. The species were sown four weeks before the start of recordings.

2.2.2 Beetles

Pterostichus melanarius were collected at the end of September 2009 in rye and oilseed radish at the Droevendaal farm using pitfall traps. Beetles were stored in containers (45x30x15cm) on a substrate of moist potting soil in a climate cabinet with a 12:12 h L:D photoperiod and a 18:12°C L:D temperature regime, about 200 beetles per container. Over the course of 4 days the photoperiod in the climate cabinet was reversed in two steps of 6 hours. This reversed the activity period of *P. melanarius* and enabled recording during working hours. On 12 October, the temperature regime in the climate cabinet was adjusted to the temperature regime in the greenhouse (20:15°C L:D). Beetles in the containers were fed frozen fly maggots (*Lucilia caesar*) once every week.

Each week, a random sample of about 100 beetles was taken from the containers. These beetles were sexed and transferred to individual plastic cups (Ø 6cm, 6cm height) containing some potting soil. Beetles in half of the cups were fed 1-2 maggots twice a week (fed beetles); the other beetles were deprived of food for at least one week before recording (starved beetles).

2.2.3 Video recordings

Video recordings were made from 12 to 20 October 2009 in the dark with a near-infrared radiation source (IR-880/12, 880 nm) (c-tac, Winsen, Germany). Images were captured using a digital camera (Imaging Development Systems GmbH, Obersulm, Germany: uEye UI-

1480RE (2560x1920)) from which the infra-red cut filter was removed. To make beetles visible for the camera a small auto-adhesive retro-reflector (35mm², ~5mg; 3M8850, 3M Leiden, The Netherlands) was attached to the elytra (see Chapter 2)(Allema et al. 2012).

2.2.4 Processing position data

Position data were extracted from the digital images by software written in Matlab R2009a (The MathWorks). Movement tracks were constructed by first excluding all position data that were inside a 10 cm zone from the arena's edge to avoid edge effects caused by wall-following behaviour (Creed Jr and Miller 1990). Also position changes of less than 0.3 cm were excluded, as these could have been caused by recording error. Next, the position data from the arena's interior were grouped into tracks. A track started when a beetle entered the arena's interior from the edge zone and ended when the beetle returned to the edge zone. A track also ended when the beetle was invisible for more than 20s. Positions within tracks were aggregated into moves using a data reduction method described by Turchin (1998, p. 132). In this method a chosen distance Δz defines a band width around each move and successive positions within the band are considered to be part of the same move. The first position outside this band defines a new move (Turchin 1998). Effectively, Δz determines the resolution at which positions are aggregated. For $\Delta z = 0$, all original positions are retained, whereas for a large Δz all positions are aggregated into a single move (Chapter 2). We used a resolution of $\Delta z = 1.6$ cm, which was large enough to prevent autocorrelation in the movement parameters and small enough to retain detail in the movement path.

2.2.5 Analysis of moves

Beetles that made fewer than 50 moves ($N = 26$) were excluded from the analysis because the calculated movement parameters, especially the mean cosine of turning angles (Batschelet 1981) would be inaccurate. For the remaining beetles (48 starved, 49 fed) we calculated average move length m_1 (cm), average squared move length m_2 (cm²), average move duration τ (s), mean cosine of turning angles (change in direction between subsequent moves in the interval $(-\pi, \pi)$ ψ (-), average velocity v (cm s⁻¹), and motility μ (cm² s⁻¹). Periods that beetles were invisible or visible but not moving were included in the time duration of a move. Motility was calculated for each beetle from the above movement parameters using a formula derived from the Patlak equation Turchin (1998, p. 102):

$$\mu = \frac{m_2 - \psi m_2 + 2\psi m_1^2}{4\tau(1-\psi)} \quad \text{eqn 8}$$

Table 1 Model selection among variants of the *Fokker-Planck* diffusion model describing beetle dispersal in the field experiment. A single parameter value is shown when habitats were not distinguished in a model variant. The value of π_1 is 1 throughout. If no value for π_2 is shown, it was set to 1 and not included in the calibration. The negative log-likelihood (NLL) is a measure of the goodness of fit of the model to the data. Δ AIC is the difference in Akaike's information criterion between a model variant and the model variant with most support of the data (model 1). Models variants of which the Δ AIC is smaller than two are considered to have equal support from the data.

Model parameters								
Model	NLL	Δ AIC	μ_1 ($\text{m}^2 \text{d}^{-1}$)	μ_2 ($\text{m}^2 \text{d}^{-1}$)	ξ (d^{-1})	ω_0 (m^{-2})	ω_1 (m^{-2})	π_2 (-)
1	944.0	0.0	215		0.066	0.17	0.09	1.5
2	944.0	2.0	218	212	0.066	0.17	0.09	1.5
3	948.9	7.9	216		0.066	0.15	0.09	
4	949.0	10.0	228	220	0.065	0.15	0.09	
5	959.5	29.1	180		0.071	0.13		1.2
6	960.7	29.6	183		0.071	0.12		
7	959.5	31.1	175	187	0.071	0.13		1.2
8	960.7	31.5	175	194	0.071	0.12		
9	997.3	104.6	217			1.46	0.35	1.8
10	997.3	106.6	219	216		1.47	0.35	1.8
11	1000.9	111.9	165	288		1.27	0.35	
12	1002.1	112.3	214			1.25	0.35	
13	1023.2	154.6	200				0.95	1.5
14	1023.4	154.8	140	316			0.89	
15	1022.7	155.4	159	256			0.94	1.3
16	1025.5	157.1	202				0.86	

μ_1 : motility in oil-radish; μ_2 : motility in rye; ξ : relative loss rate due to removal other than recapture (e.g. mark wear and mortality); ω_0 : trap-coefficient for trapping stations without screens; ω_1 : trap-coefficient for trapping stations with screens; π_1 : multiplication factor of the flux of beetles from oil-radish to rye; π_2 : multiplication factor of the flux of beetles from rye to oil-radish.

Population motility was calculated as the average motility of individual beetles. The motility estimate that we obtained in the arenas was extrapolated to field scale by assuming that the movement pattern observed in the arenas was representative for the movement pattern during an activity period of 11 h per 24 hours, the time between sunset and sunrise in the Netherlands in September. Accordingly, motility obtained in the arenas ($\text{cm}^2 \text{s}^{-1}$) was multiplied by $11 \times 3600 \times 10^{-4} = 3.96$ to obtain daily motility ($\text{m}^2 \text{day}^{-1}$).

2.2.6 Statistical analysis

A Generalized Linear Mixed Model (GLMM) (GenStat Fourteenth Edition, VSN International Ltd) was used to analyse the effects of feeding level, gender and crop type on the time that beetles spent in the arena's interior and on the movement parameters m_1 , ψ , τ , m_2 , v , and μ . Date of recording was included in the model as a random term. To stabilize the variance in the data, log- and square root transformations were used and two outliers in the data of

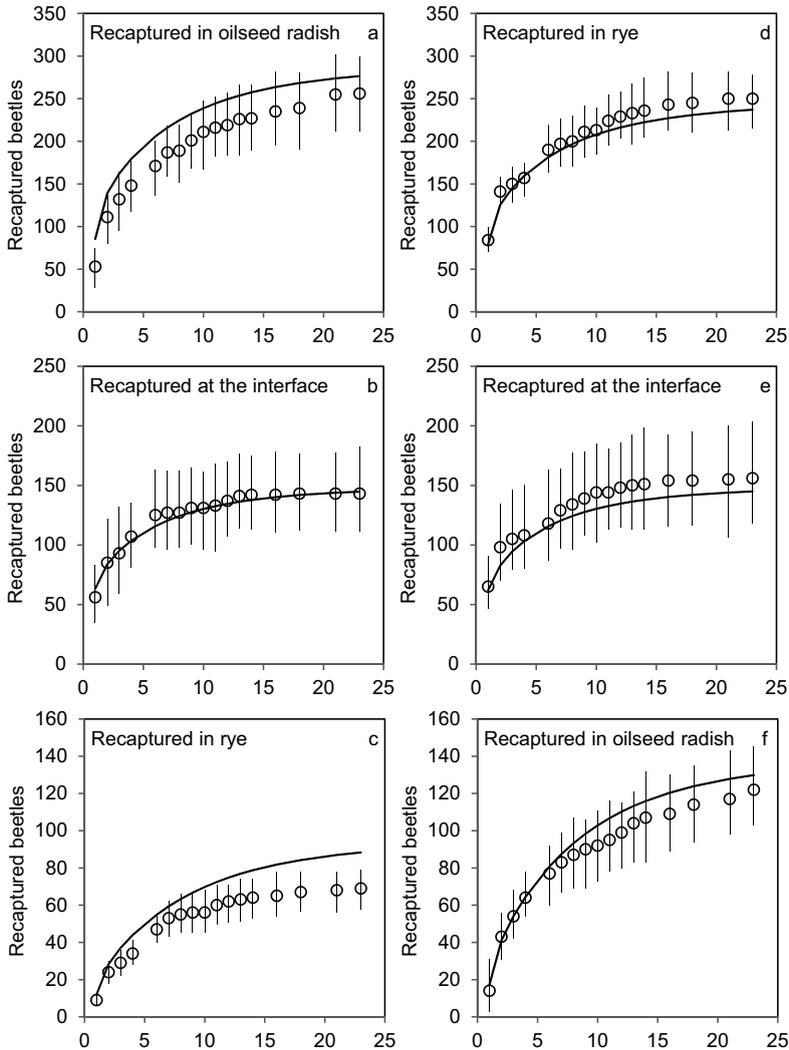


Fig. 3. Observed (o) and predicted (line) cumulative number of recaptured *P. melanarius* as a function of time. Predicted values were simulated with the calibrated model that had most support from the data (model 1, Table 1). Panels on the left (a-c) are for beetles released in oilseed radish, on the right (d-f) for beetles released in rye. Error-bars show the 95% confidence interval of the observations.

move duration were removed ($\tau = 17$ s and $\tau = 26$ s). The F-statistic was used as a criterion for significance at a 95% confidence level. The total time that beetles spent in the arena's interior was calculated as the sum of path durations (trajectory from edge to edge via the interior). A two-sample Welch's t-test was used to test for a difference in the mean frequency of beetles moving from the arena's edge zone to the interior, and for a difference in the mean path duration in the arena's interior. A square root transformation was used to homogenize the variances of the data on path duration.

3 Results

3.1 Field experiment

Out of the 2030 released beetles, 996 were recaptured over a period of 23 days. Of the beetles released in oilseed radish, 7% were recaptured in rye, and of those released in rye, 12% were recaptured in oilseed radish, indicating greater numbers moving from rye to oilseed radish than vice versa.

Motility of beetles in the slow-release boundary μ_0 and the negative-binomial dispersion parameter k were calibrated using variant 4 (Table 1) of the Fokker-Planck model resulting in estimates of $\mu_0 = 4.1 \text{ m}^2 \text{ d}^{-1}$ and $k = 3.1$. Preliminary calibrations showed that model

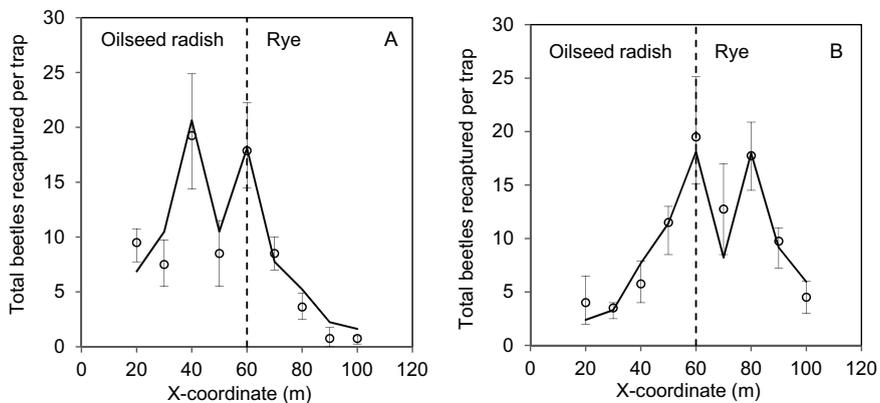


Fig. 4. Distribution of observed (o) and predicted (line) number of *P. melanarius* recaptured along the length of the experimental field, cumulated over time and over the width of the field for (a) beetles released in oilseed radish at 50 m and (b) beetles released in rye at 70 m. Predicted values are simulated with the model that had most support from the data (model 1, Table 1). The error-bars show the 95% CI of the observations.

credibility depended more on the ratio of the parameters π_1 and π_2 than on their absolute values. For example, optimizing both π_1 and π_2 of model 1 (Table 1) resulted in an AIC that was 1.9 higher than the AIC of the model variant in which only π_2 was optimized, i.e. a small decrease in negative log-likelihood was more than offset by an increase in the penalty for the extra parameter. We concluded that the data did not support the determination of two flux modifiers. Instead, we set π_1 to one and calibrated π_2 .

The greatest support by the data was for model 1 (Table 1) with a single motility parameter ($\mu = 215 \text{ m}^2 \text{ d}^{-1}$; identical for oilseed radish and rye), a relative loss rate of $\xi = 0.066 \text{ d}^{-1}$, trapping efficiencies $\omega_0 = 0.17 \text{ m}^{-2}$ without screens and $\omega_1 = 0.09$ with screens, and a flux modifier from rye to oilseed radish $\pi_2 = 1.5$, indicating preference for oilseed radish.

Comparison of predictions with model 1 and observations showed that for beetles released in oilseed radish the model slightly overestimated the number of beetles recaptured in oilseed radish (Fig. 3a) and in rye (Fig. 3c), but gave an accurate prediction of the number of beetles recaptured at the interface (Fig. 3b). For beetles released in rye and recaptured in both crops and at the crop interface the predicted cumulative number of beetles through time was well within the 95% confidence interval of the data (Fig. 3d-f). The distribution of recaptures along the length of the field, cumulated over time and over the width of the field, was well within the 95% confidence interval of the data both for the beetles released in oilseed radish and in rye (Fig. 4a and 4b).

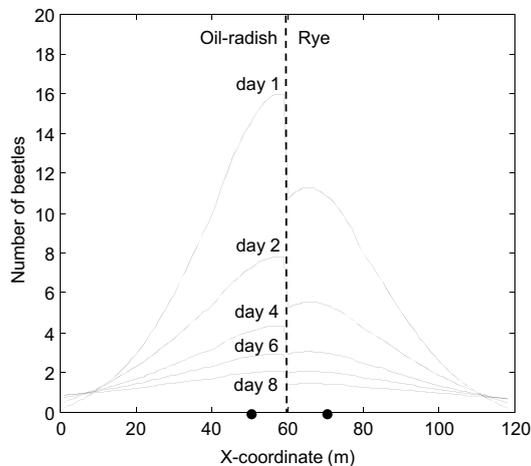


Fig. 5. Distribution of *P. melanarius* along the length of the field over time simulated with the model that had most support from the data (model 1, Table 1). The Y-axis represents the total number of beetles over the width of the field. On day 0, 1015 beetles were released at each black dot. Number of beetles in the slow-release margins that surround the field are not shown.

Table 2 Average movement parameters (\pm se) of *P. melanarius* in an arena experiment with hunger level, gender and crop species as factors. Number of observations per factor is indicated in the column headings. Beetles were recorded for 50 min in arenas of 5 m². p-values in bold indicate significant differences ($p < 0.05$) between treatment groups

	Starved (N = 48)	Fed (N = 49)	d.d.f.	F^2	p two-sided
Time in arena's interior (min)	15.8 \pm 1.2	11.6 \pm 0.8	91.7	8.6	0.004
Move length m_1 (cm)	10.9 \pm 0.4	11.7 \pm 0.4	90.7	7.3	0.008
Angular dispersion ψ (-)	0.707 \pm 0.011	0.700 \pm 0.013	92.4	0.01	0.940
Move duration τ (s)	7.3 \pm 0.5	5.6 \pm 0.2	89.5	9.8	0.002
Squared move length m_2 (cm ²)	165.0 \pm 11.9	188.3 \pm 12.3	90.4	7.0	0.01
Speed v (cm s ⁻¹)	1.7 \pm 0.1	2.2 \pm 0.1	92.9	12.6	<0.001
Motility μ (cm ² s ⁻¹)	38.3 \pm 5.1	50.3 \pm 6.8	91.3	8.8	0.004
Daily motility μ (m ² d ⁻¹)	151.7 \pm 20.2	199.2 \pm 26.9			
	Female (N = 50)	Male (N = 47)		F^2	p two-sided
Time in arena's interior (min)	14.0 \pm 1.0	13.4 \pm 1.2	91.8	0.7	0.409
Move length m_1 (cm)	11.2 \pm 0.3	11.4 \pm 0.5	90.4	0.2	0.704
Angular dispersion ψ (-)	0.701 \pm 0.009	0.706 \pm 0.014	92.2	0.2	0.650
Move duration τ (s)	6.2 \pm 0.2	6.6 \pm 0.6	88.2	1.3	0.260
Squared move length m_2 (cm ²)	172.2 \pm 8.2	181.8 \pm 15.5	90.1	0.2	0.702
Speed v (cm s ⁻¹)	1.9 \pm 0.1	2.1 \pm 0.1	92.8	2.1	0.154
Motility μ (cm ² s ⁻¹)	37.1 \pm 2.9	52.2 \pm 8.2	91.0	0.2	0.696
Daily motility μ (m ² d ⁻¹)	146.9 \pm 11.5	206.7 \pm 32.5			
	Oilseed radish (N = 53)	Rye (N = 44)		F^2	p two-sided
Time in arena's interior (min)	15.6 \pm 1.1	11.4 \pm 1.0	87.3	12.2	<0.001
Move length m_1 (cm)	11.5 \pm 0.3	11.1 \pm 0.4	85.7	0.4	0.521
Angular dispersion ψ (-)	0.704 \pm 0.011	0.702 \pm 0.014	86.3	0	0.906
Move duration τ (s)	6.6 \pm 0.4	6.3 \pm 0.4	85.7	0.5	0.483
Squared move length m_2 (cm ²)	180.0 \pm 9.5	173.0 \pm 15.2	85.7	0.9	0.352
Speed v (cm s ⁻¹)	2.0 \pm 0.1	2.0 \pm 0.1	86.4	0.1	0.737
Motility μ (cm ² s ⁻¹)	41.5 \pm 4.1	47.9 \pm 8.1	85.9	0	0.952
Daily motility μ (m ² d ⁻¹)	164.3 \pm 16.2	189.7 \pm 32.1			

[†]F statistic, n.d.f. = 1 for all tests

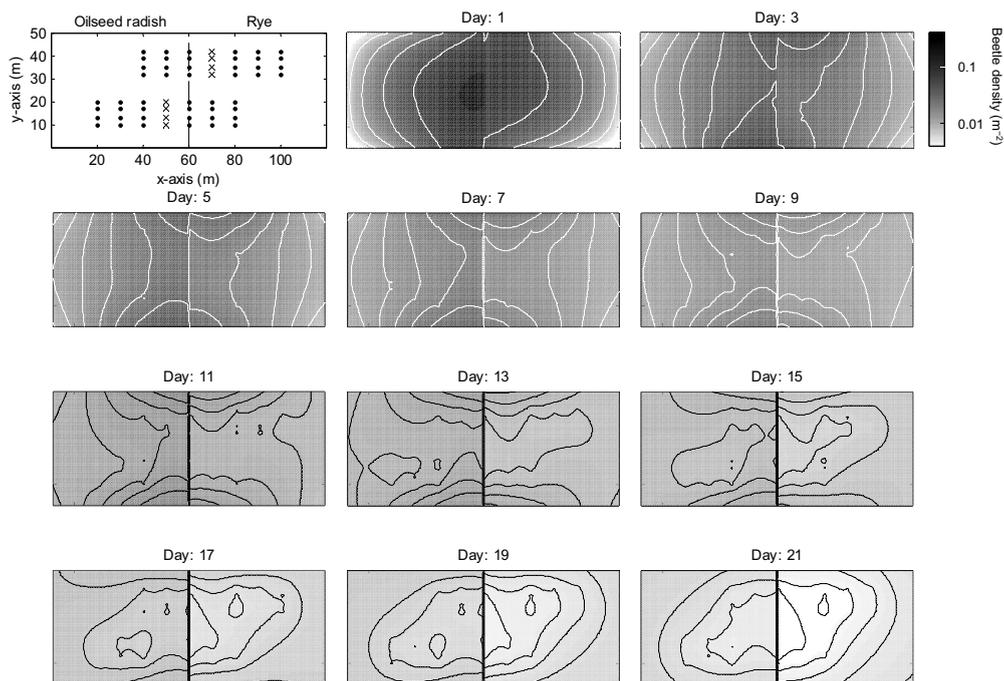


Fig. 6. Time evolution of the distribution of *Pterostichus melanarius* in two adjacent crops simulated with a Fokker-Planck diffusion model (model 1, Table 1) that had a common value of motility for both crops ($215 \text{ m}^2 \text{ d}^{-1}$) and preferential movement at the interface equivalent to a beetle on the interface moving to oilseed radish with a probability of 0.60 and moving to rye with a probability of 0.40. Beetle densities varied between 0.42 m^{-2} on day 1 to 0.008 m^{-2} on day 21. Beetles densities in the slow-release margins that surrounded the experimental field were omitted. Crosses and dots in the upper left panel mark the locations at which beetles in the model were released and recaptured, respectively.

Simulations with model 1 showed an abrupt increase of beetles in oilseed radish close to the interface and a rapid decline of beetle numbers through time (Figs 5 and 6). The ratio of the number of beetles just left (oil seed radish) to just right (rye) of the interface was constant at 1.5. A substantial proportion of dispersing beetles reached the field edges in the simulations. On day 1, 757 of the released beetles (37%) were still in the experimental field (Fig. 7). The remaining beetles had moved into either the north or south boundaries (39%), were recaptured (16%), were lost due to mark wear or mortality (7%) or had moved into the east or west slow-release boundaries (1%) (Fig. 7). By the end of the experiment most beetles had been recaptured or lost due to e.g. mark wear or mortality, and only a small fraction was still in the field or in the slow-release boundaries (Fig. 7).

3.2 Arena experiment

GLMM analysis demonstrated a significant effect ($p < 0.05$) of feeding level on all movement parameters except angular dispersion, and no significant effects of gender or crop species (Table 2). Motility, move length, squared move length, move duration and speed were significantly higher for fed than for starved beetles (Fig. 8, Table 2). Average daily motility of beetles in the arenas ranged between 147 and 207 $\text{m}^2 \text{d}^{-1}$ (Table 2), which was similar to the motility of beetles in the field experiment (215 $\text{m}^2 \text{d}^{-1}$).

During the 50 min recording period beetles moved between the edge-zone and the arena's interior (Fig. 8). GLMM analysis demonstrated a significant effect of feeding level and crop type, but not of gender on the total time beetles spent in the arena's interior (Table 2). Beetles spent more time in the interior of oilseed radish than of rye because beetles moved significantly more often from the edge into the interior of oilseed radish (mean \pm se: 17.0 \pm 1.1 times) than of rye (13.5 \pm 1.0 times) (t-test: $t = 2.3$, d.f. = 95, $p = 0.024$). Furthermore, the average path duration in the interior was also greater in oilseed radish than in rye (oilseed radish: mean \pm se: 1.9 \pm 0.9 min; rye: 1.1 \pm 0.1 min; t-test: 7.1, d.f. = 93.2, $p < 0.001$). These results indicate a preference of beetles for oilseed radish over rye and an inclination of beetles to stay in oilseed radish. Between fed and starved beetles there was no significant

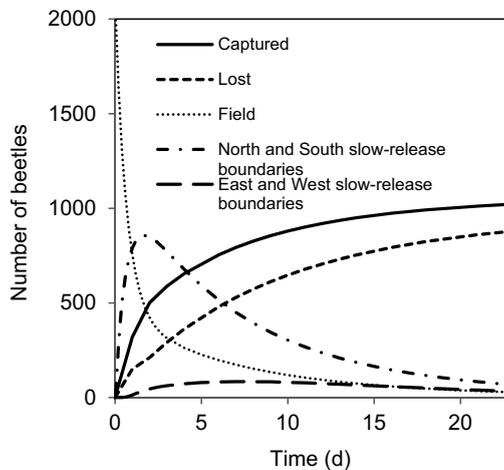


Fig. 7. Simulated change in time of the number of marked beetles in the field and the slow-release boundaries, and the change in number of beetles that were either captured or lost due to mark wear or death. Simulations were made with the model that had most support from the data (model 1, Table 1). At Time = 0, a total of 2030 virtual beetles were released.

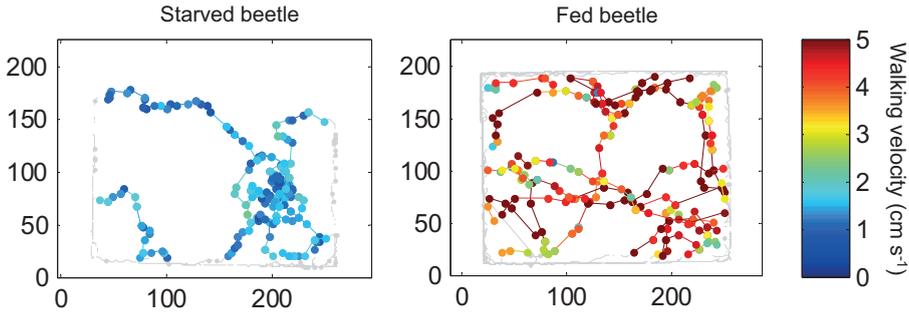


Fig. 8. Examples of movement tracks for a starved *Pterostichus melanarius* beetle with low motility ($7 \text{ cm}^2 \text{ s}^{-1}$; left) and for a fed beetle with a high motility ($88 \text{ cm}^2 \text{ s}^{-1}$; right). The total time spent in the arena's interior was 24.8 min for the starved and 11.7 min for the fed beetle. Moves in the 10 cm edge zone are represented by thin grey lines.

difference in the frequency of moves from the edge into the interior (mean \pm se: 15.0 ± 1.1 times for starved beetles and 15.9 ± 1.1 for fed beetles; t-test: $t = 0.6$, d.f. = 95, $p = 0.554$). The mean path duration of starved beetles in the arena's interior was significantly greater than the mean path duration of fed beetles (mean \pm se: 2.2 ± 1.0 min for starved beetles; 0.8 ± 0.07 min for fed beetles; t-test: $t = 2.1$, d.f. = 95, $p = 0.039$).

4 Discussion

This study provides evidence for preferential movement behaviour at habitat interfaces by a ground-dwelling arthropod predator, based on a combination of field and laboratory data. Motility was neither different between crops in the field nor in the experimental arenas. The more frequent movement from oilseed radish to rye can thus be attributed to preferential behaviour at the interface. The arena observations support this conclusion from a mechanistic point of view. In the arena beetles entered more frequently into the vegetated zone and were more reluctant to leave this zone in oilseed radish than in rye. The preference of beetles to move to oilseed radish as compared to rye can thus be explained by attraction towards oilseed radish and a higher inclination of beetles to stay in this crop. This greater preference for oilseed radish compared to rye may be caused by a response of *P. melanarius* to differences in food resources between the crops, plant odours (Tréfás et al. 2001) or differences in micro-climate (Chapman et al. 1999, Tréfás and Van Lenteren 2008). While plant odours may attract insects over larger distances, a change in movement behaviour in response to micro-climate operates at a local scale.

The motility of beetles estimated from our field data corresponded well with the motility of beetles in the arenas scaled-up to daily motility. In the field study a single value for motility was estimated using inverse modelling with a Fokker-Planck diffusion model, describing the average rate of population spread over a period of 23 days. In the arenas motility was calculated for individual beetles based on 50 min observation time. The close correspondence in motility between the field and arena indicates that averaging over individuals' motility is a good predictor for the rate of population spread of a population. This approach to scaling-up is fundamentally different from earlier methods of scaling-up that simulate individual behaviour from empirical distributions of observational data on step length and turning angles (e.g. Kindvall 1999, Morales and Ellner 2002, Chapman et al. 2007) or from theoretical distributions fitted to these data (e.g. Sabelis 1981, Mols 1993, Firle et al. 1998). In either case, the distributions of step lengths and turning angles are determined from movement behaviour pooled over individuals. Such pooling of movement data ignores the variation in movement behaviour between individuals, which may cause an underestimation of the true rate of population spread, due to the non-linear (convex) relation between movement parameters (e.g. step lengths and turning angles) and motility (i.e. the rate of population spread) in equation 8. The error made by applying a function to the mean of variable inputs rather than – as it should be done – to each input and then calculate the mean output, is known as “Jensen’s inequality” (Kuczma 2009). The error caused by pooling movement data can be large. For instance, in our experiments motility of starved beetles was $151.7 \text{ m}^2 \text{ d}^{-1}$, but would have been $106.2 \text{ m}^2 \text{ d}^{-1}$ if motility had been calculated from movement data pooled over individual beetles. This underestimation of population spread may explain why Firle et al. (1998) and Morales and Ellner (2002) needed to add behavioural variation in the form of switching between behavioural modes in order to obtain a good fit between the simulations and empirical data. The need to include individual variation in movement in population models has been emphasized before (Firle et al. 1998, Hawkes 2009). Here, we illustrate from a mathematical point of view how neglecting this variation may lead to a mismatch between individual movement data and population spread.

An important consideration in scaling-up movement behaviour from a small scale arena to field scale was the time duration that beetles were assumed to be active, here taken as the time window length from sunset till sunrise. The assumption made here is consistent with observations on activity period of *P. melanarius* observed in the behavioural experiment in chapter 2 (results not shown).

Gender did not influence motility of beetles in the experimental arenas, which is in accordance with previous observations (Chapter 3) (Allema chp3) (Allema chp3). The higher

motility for fed beetles in the arenas contrasts with the majority of other studies in which satiation reduced movement activity (Wallin and Ekbohm 1988, Wallin 1991, Mols 1993, Wallin and Ekbohm 1994, Fournier and Loreau 2001, Griffiths et al. 2008). Reduced movement activity caused by satiation is proposed as a mechanism to arrest organisms in patches with high prey availability (Bell 1990). The opposite behaviour displayed by beetles in our arenas may point to another mechanism, e.g. energy depletion.

The boundaries of the field were modelled as slow-release boundaries for which a specific motility parameter was calibrated. Simulation results showed that due to their high motility, many beetles reached the north and south boundaries of the field, which first acted as sinks and later as sources of beetles (Fig. 7), just as could happen in a real landscape. The north and south boundaries consisted of six-meter wide grass strips which are known to slow down movement of carabid beetles (Frampton et al. 1995, Mauremooto et al. 1995, García et al. 2000, Fournier and Loreau 2002). The predicted accumulation of beetles in the margins by the model is thus a realistic reflection of the experimental landscape setting.

In conclusion, our study provides details on the processes that lead to pattern formation of arthropods in agricultural land and on scaling up movement behaviour to population spread. We show that the interface between crop habitats have implications for the dispersal and distribution of carabids in adjacent crops. The approach provides a framework for evaluation of movement within and across habitats in more complex agricultural landscapes.

Acknowledgements

We thank Dine Volker for technical support, Jacques Withagen for statistical advice and Felix Bianchi for valuable comments on an earlier version of this manuscript. Special thanks go to Herman Berghuijs and Anne Balkema who contributed to this work as part of their Msc thesis research. This project was financially supported by strategic research funds of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation and is part of the strategic research program “Sustainable spatial development of ecosystems, landscapes, seas and regions” which is funded by the Dutch Ministry of Agriculture, Nature Conservation and Food Quality, and carried out by Wageningen University Research Centre (KB-01-008-024-ALT).

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Chapter 5

Effect of habitat heterogeneity on dispersal of *Pterostichus melanarius* (Coleoptera: Carabidae) in a landscape mosaic identified using mark-recapture data and diffusion models

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Joop van Lenteren

Abstract

Distribution of animals in time and space is affected by their dispersal capacity and by habitat heterogeneity at landscape level. Here we studied the effect of habitat composition and configuration on within season dispersal behaviour of *Pterostichus melanarius*, an arthropod ground predator of invertebrates, including agricultural pests. Dispersal behaviour was studied in a mark-recapture experiment in an agricultural landscape mosaic comprising perennial strips and different crop species with distinct tillage management. Food availability per habitat was assessed from the weight of naturally occurring beetles. Model selection in a set of diffusion models that included motility, interface-mediated behaviour and beetle loss was used to identify functionally different habitat units. Semi-natural grass margins were functionally different from the crop habitats. In the margins motility was lower than in the crop habitats, and at the crop-margin interface more beetles moved towards the crop than to the margin, meaning that margins acted as barriers for dispersal. In the crop habitats motility differed between fields but no consistent relations were found with crop species, food availability or tillage. Based on the motility in crop habitats we predict *P. melanarius* to disperse over a distance of about 100 – 160 m during a growing season. Given this range we expect little redistribution of beetles between fields within a growing season, meaning that the success of biological control by this species is more dependent on field management affecting local population dynamics than on habitat heterogeneity.

1 Introduction

Distribution of animals in time and space is affected by their dispersal capacity and by habitat heterogeneity at landscape level. Habitat heterogeneity can be interpreted in terms of the variation in land use and is then referred to as compositional heterogeneity, or in terms of spatial arrangement of land use which is denoted as configurational heterogeneity (Turner 2005). Management of landscapes for greater provisioning of ecosystem services requires a functional interpretation of habitat heterogeneity (Fahrig et al. 2011), which links ecosystem services to ecosystem functions and to species traits.

Agricultural landscapes comprise agricultural fields and semi-natural landscape elements. Both types of habitat provide resources that support beneficial species suppressing agricultural pests (Bianchi et al. 2006; Blitzer et al. 2012). Over the past decades, agro-landscapes have seen an increasing fragmentation and homogenization, which has resulted in a sharp biodiversity decline (Matson et al. 1997). There is increasing interest in reversing these trends and the ecosystem service of pest suppression provides a logical connection between agricultural interests and biodiversity restoration. Redesign of landscapes for pest suppression requires design rules and norms for the size of landscape elements and the distances between them (Steingröver et al. 2010). Strengthening the scientific basis of these norms is important to enhance effectiveness of financial resource use and to maintain momentum among land managers. Here we address dispersal of an arthropod predator of agricultural pests in an agricultural landscape.

Arthropod dispersal has mostly been studied for species with a distinct habitat preference. Ovaskainen (2004) and Ovaskainen (2008a; 2008b), for example, studied butterflies moving between habitat patches in a landscape matrix of less suitable habitat. Reeve et al. (2008) studied plant hopper movement in paired habitat combinations consisting of the plant hopper's host plant cordgrass and the major habitat types in its natural environment brome and mudflat. The composition of the matrix habitat is considered to affect arthropod dispersal rate (e.g. Ricketts 2001) and together with habitat quality determines the probability of an individual to leave a habitat patch (Haynes and Cronin 2004). The compositional and configurational heterogeneity of a landscape may thus influence arthropod abundance and distribution in space and time. The consequences of compositional heterogeneity and habitat quality for dispersal of arthropods with a wide habitat range have received limited attention thus far.

Carabid beetles are an abundant group of arthropod predators in arable land (Kromp 1999) and an important component of the beneficial fauna for biological control of crop pests and weed seeds (e.g. Sunderland 2002; Westerman et al. 2003). Dispersal of carabid beetles has been studied in natural and agricultural systems. Methods of study range from detailed observations on movement trajectories of individual beetles in 5 m² arenas (Chapter 3, Chapter 4) to measurements on average displacement distances using mark-recapture in landscapes of 64 ha (Holland et al. 2004).

In a review of the literature (Table A1) we found that carabid dispersal in agricultural habitats has most often been studied in cereals, which have been compared with a range of other crop species, including maize, potato, perennial ley, beans, oilseed-radish, or with (semi-) natural habitats comprising hedgerows, shelterbelts, deciduous woods and grassy strips. Some studies addressed the effect of land management (harvest, harrowing) on carabid movement in cereals. Most studies reported a difference among habitat types in movement pattern, movement rate, displacement distance or rate of population spread. Differences among habitats have been attributed to habitat preference (Wallin 1986), prey availability (Bommarco and Fagan 2002), plant density (Thomas et al. 2006) and land use intensity (Kennedy 1994). Within cereals, differences in movement were related to activity density (Holland et al. 2004) and aphid density in combination with feeding level of beetles (Wallin and Ekbohm 1994). In comparisons between adjacent habitats significant bias in movement direction has been observed. Beetles moved more frequently from cereals to maize, beans or oilseed-radish than in the opposite direction (Duelli et al. 1990; Thomas et al. 2006; Chapter 4). Between cereals and grassy strips, on the contrary, beetles moved more frequently from the strips towards cereals (Kujawa et al. 2006). Hedgerows and grass margins appeared barriers for movement for carabids (Thomas et al. 1998; García et al. 2000), the permeability of which was related to satiation of beetles (Frampton et al. 1995; Mauremooto et al. 1995).

The results in Table A1 thus show that to describe movement in an agricultural landscape information on dispersal behaviour in crops and in semi-natural habitats needs to be integrated with information on behaviour at interfaces between these habitats and with satiation of beetles. A growing number of studies reveal that diffusion models that classify the landscape in distinct habitat types provide a useful framework for such integration (Ovaskainen 2004; Arellano et al. 2008; Ovaskainen et al. 2008a; Ovaskainen et al. 2008b; Reeve et al. 2008; Reeve and Cronin 2010; Chapter 4). In diffusion models the effects of compositional heterogeneity of a landscape on behaviour and fitness of individuals can be

quantified in parameters such as motility, preference at a habitat interface and mortality, and the habitat-specificity of these parameters can be tested. In Chapter 4, for example, we tested for the habitat specificity of motility for the carabid beetle *Pterostichus melanarius* and found no difference in motility between oilseed-radish and rye, but did find a significant effect of the interface between these habitats on immigration rates into each crop.

Aim of this paper is to quantify dispersal behaviour of the generalist predator *Pterostichus melanarius* (Coleoptera: Carabidae) across a set of agricultural fields separated by semi-natural elements, together constituting a mosaic of seven spatial units with distinct land use. *Pterostichus melanarius* has a broad habitat range and is a characteristic inhabitant of arable fields in Europe (Thiele 1977). Adult beetles eat a broad range of epigeal invertebrates, including at least fourteen pest species belonging to Mollusca, Coleoptera, Diptera, Homoptera and Lepidoptera (Sunderland 2002). We quantify motility of fed and starved *P. melanarius* within each spatial unit of the landscape mosaic and preference at the interface of two units, and use model selection on a set of diffusion models to identify functionally different units. In doing so, we characterize the compositional heterogeneity of the landscape mosaic comprising cultivated and perennial areas, differences in crop species, tillage regime and food availability in terms of functional heterogeneity.

2 Methods

2.1. Experimental setting

A mark-recapture study was laid out in the summer of 2010 at the organic experimental farm Droevendaal (51°5'N, 05°40'E, 20 m above sea level, Wageningen, The Netherlands). The farm is characterized by sandy soils with about 3% organic matter and fields of about 2 ha separated by perennial field margins. Beetles were recaptured in a trapping area covering seven spatial units with distinct land-use including crops and semi-natural field margins (Fig. 1). Margin 1 was 7 m wide and consisted of tall grasses, herbs and a six year old hedgerow (see picture f in the appendix). Margin 2 was 6.5 m wide and consisted of a 4 m wide strip with similar vegetation as in margin 1 but without a hedgerow and a 2.5 m wide strip with grass/clover (see picture g in the appendix). Fields 1 to 4 consisted of spring barley (*Hordeum vulgare*, cv. Quench), and field 5 consisted of yellow mustard (*Sinapis alba*, cv. Achilles) (see picture h in the appendix). Half of the fields with barley were not ploughed during field preparation, which we considered as a trait of compositional heterogeneity (Fig. 1).

Adult beetles for release in the mark-recapture study were collected from pitfall traps in fields 2 and 3 (Fig. 1) at the end of June 2010. Beetles were stored in containers (45x30x15 cm; 400 beetles per container) on a substrate of moist potting soil in a dark room at 12°C. Only females were used for the mark-recapture study. During storage, beetles were fed frozen fly maggots (*Lucilia caesar*). Over a period of three weeks half of the beetles were fed a total of 22 mg of maggots per beetle (starved beetles); the other half (fed beetles) received twice a week 22 mg of maggots per beetle, so in total 132 mg per beetle over three weeks. On 21 July, the average body weight \pm se of starved and fed beetles was 0.14 ± 0.004 g and 0.17 ± 0.004 g, respectively.

Beetles were marked on their elytra with nail polish (OPI Nail lacquer) of different colours to indicate the beetle's diet treatment and designated location of release (line A, B or C; Fig. 1). On 20 July at 7 p.m. release trays (37 x 56 x 7 cm) with in total 3665 appropriately marked female beetles were placed on the designated 5 release points per release line (for the number of beetles released per release line see Table 1). Beetles could escape from the trays through small holes at the soil surface. The following morning almost all beetles had left the trays; the few remaining individuals were released manually.

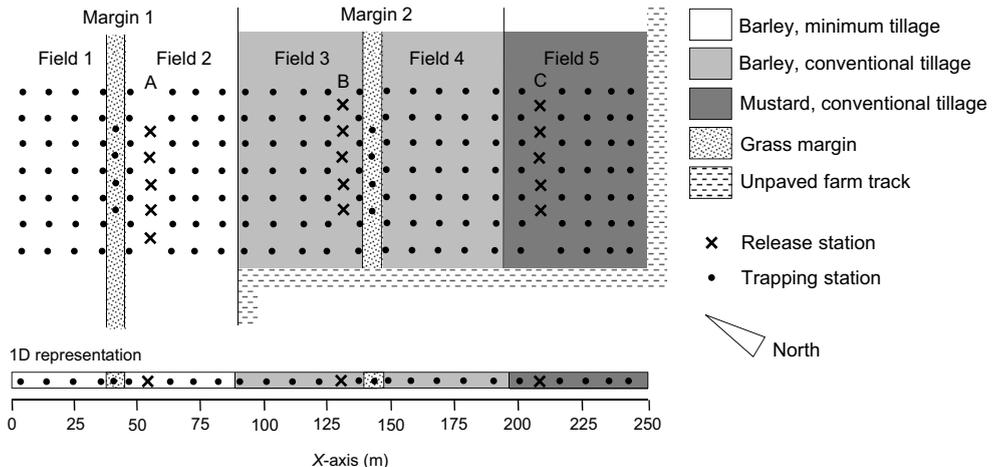


Fig. 1 Spatial layout of the trapping and release stations in a cross section of a small scale landscape consisting of different crops and field margin habitats. The field margin 1 consisted of tall grasses, herbs and a six year old hedgerow. The field margin 2 had the same vegetation as 1, except for the hedgerow. Below is the one-dimensional representation of the landscape that is used for model calibration.

Table 1 Number of fed and starved beetles recaptured per habitat as a function of release site and feeding level. Number of released beetles between parentheses. A is for beetles released in field 2, B for beetles released in field 3 and C for beetles released in field 5 (see Fig. 1).

Feeding level	A		B		C		Total (3665)
	Fed (720)	Starved (620)	Fed (680)	Starved (465)	Fed (585)	Starved (595)	
Field 1	4	8	0	0	0	0	12
Margin 1	2	3	0	0	0	0	5
Field 2	142	93	9	7	0	0	251
Field 3	19	5	166	101	1	1	293
Margin 2	0	0	13	5	0	0	18
Field 4	0	1	30	13	20	23	87
Field 5	0	2	0	1	90	114	207
Total	167	112	218	127	111	138	873

Recaptures were made in a grid of pitfall traps that were spaced 9-17 m apart in the East-West direction and 10 meter in the North-South direction. At each trapping station two pitfall traps were placed at one meter distance from each other. The recaptures made in these traps were added. The traps consisted of inner and outer plastic cups (\varnothing 8 ½ cm) and a black plastic disk to provide cover from rain. During the first two weeks after release, traps were emptied every working day. Thereafter, until 11 August, traps were emptied every 2-6 days. Due to high weed incidence in field 1, the harvest of the crop was advanced and sampling could only take place until 30 July.

2.2 Analysis of mark-recapture data

2.2.1 Fokker-Planck diffusion model

The mark-recapture data was analysed following the procedure in Chapter 4 using a Fokker-Planck diffusion model and model selection. The aim of model selection was to find a model with the least parameters needed to describe the distribution pattern of beetles over time. The most comprehensive model that was calibrated (the 'full' model) accounted for (1) random movement, or motility per habitat, (2) behaviour at each habitat interface, (3) loss of beetles due to trapping, (4) loss of beetles due to mortality and mark wear and (5) the distinction between fed and starved beetles. Because beetles were released from a line source and were recaptured at lines parallel to this source (Fig. 1), we simplified the model to a one dimensional representation of reality, which reduced the computation time needed for calibration considerably.

The one-dimensional partial differential equation for dispersal of beetles in the landscape mosaic was:

$$\frac{\partial N_i(x,t)}{\partial t} = \nabla^2 [\mu_i(x)N_i(x,t)] - \alpha_i(x)N_i(x,t) - \xi_i N_i(x,t) \quad \text{eqn 1}$$

where ∇^2 is the Laplace operator that takes the second derivative in the x direction, $\mu_i(x)$ is the motility ($\text{m}^2 \text{d}^{-1}$) at location x for fed ($i = 1$) and starved ($i = 2$) beetles; $N_i(x,t)$ is the beetle density (m^{-2}) 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; d^{-1}); and ξ_i is the relative loss rate of marked beetles due to death or mark wear (hereafter: relative loss rate; d^{-1}).

Equation 1 was solved numerically using the forward central finite difference method (Press et al 2007) on a lattice of grid cells with mesh size $\Delta x = 1$ m and reflective outer boundaries. The change in density of beetles in a grid cell with coordinate x during a time step Δt was calculated as:

$$\Delta N_i(x,t) = (I_{x,i} - (\xi_i + \alpha_i(x))N_i(x,t))\Delta t \quad \text{eqn 2}$$

where $I_{x,i}$ represent the net rate of change of fed ($i = 1$) and starved ($i = 2$) beetle density in a grid cell at location x due to fluxes over the border with adjacent cells. $I_{x,i}$ is defined as:

$$I_{x,i} = \frac{\mu_i(x-1)N_i(x-1,t) - 2\mu_i(x)N_i(x,t) + \mu_i(x+1)N_i(x+1,t)}{\Delta x^2} \quad \text{eqn 3}$$

An adjusted form of equation 3 was used for cells bordering an interface between two habitat types to allow for habitat preference of beetles when at the interface. Assuming that the interface is located at $x = \nu$ and that the cell left of the interface has the x -coordinate $\nu - \frac{1}{2}$ and the cell right of the interface has the x -coordinate $\nu + \frac{1}{2}$. The flux of beetles for the cell left of the interface is:

$$I_{\nu,i} = \frac{\mu_i(\nu - \frac{3}{2})N_i(\nu - \frac{3}{2},t) - \mu_i(\nu - \frac{1}{2})N_i(\nu - \frac{1}{2},t) - p_i\mu_i(\nu - \frac{1}{2})N_i(\nu - \frac{1}{2},t) + q_i\mu_i(\nu + \frac{1}{2})N_i(\nu + \frac{1}{2},t)}{\Delta x^2}$$

eqn 4

Here, the dimensionless flux-modifier p_i affects the flux of beetles moving from left to right,

while q_i modifies the flux of beetles in the opposite direction. Likewise, an adjustment for preferential movement direction is made for the cell at the right side of the interface. The meaning of these flux-modifiers can be understood by considering a beetle that is located exactly on the interface. Its probability of moving to the right is $p_i/(p_i+q_i)$ while its probability of moving to the left is $q_i/(p_i+q_i)$ (cf. Chapter 4). To simulate interface mediated behaviour only one of flux-modifiers needs to be calibrated while keeping the other at 1. We use a single symbol π_i to denote interface-mediated behaviour and indicate in the text for which direction (p_i or q_i) π_i is calibrated.

Relative capture rate $\alpha_i(x)$ is a linear function of $\mu_i(x)$ according to:

$$\alpha_i(x) = \begin{cases} \omega_i \mu_i(x) & \text{at trapping locations} \\ 0 & \text{at other locations} \end{cases} \quad \text{eqn 5}$$

where the constant of proportionality ω_i (m^{-2}) is the efficiency with which beetles are recaptured at the trapping stations (hereafter: trapping efficiency). The parameter calibrated to data is ω_i not α_i .

2.2.2 Model selection

The full model contained 30 parameters (for each of the two feeding levels: 7 for habitat specific motility; 6 for interface-mediated behaviour; 1 for general loss rate and 1 for trapping efficiency). Model selection was used to find the model with the smallest number of parameters that best explained the data. Model selection is a method whereby a suite of candidate models is fitted to data with maximum likelihood, and an information criterion is used to assess goodness of fit given the number of parameters used to achieve this fit, i.e. penalizing models that require many parameters to “explain” the data (Hilborn and Mangel 1997; Bolker 2008). The AIC is calculated as $2 \cdot \text{NLL} + 2 \cdot k$, in which NLL is the negative log likelihood (described below) and k the number of parameters. Models with a difference in |AIC| equal to or smaller than two are considered equivalent. This means in our case that the addition or removal of parameters did not improve model fit. Vice versa when the difference in |AIC| is larger than two the addition or removal of a parameter contributed to model fit.

Variants of equation 1 were fitted to the data by minimizing the negative log-likelihood:

$$\text{NLL} = - \sum_{t,x} \ln \left(L \left(Y_{t,x} \mid f(t,x,P) \right) \right) \quad \text{eqn 6}$$

Where L is the negative binomial likelihood of the data $Y_{t,x}$, given model predictions f at trap location x and time t , based on parameter vector P . The NLL was minimized using a differential evolution algorithm (Storn and Price 1997), implemented in reusable C++ code that is part of the COMPASS framework (Groot et al. 2012). The dispersion parameter of the negative binomial distribution was estimated once by calibration using model 2 (Table 2) and was set as a constant (1.45) during the calibration of the model variants.

The large number of parameters in the model made it impossible to compare all parameter combinations in a single model selection procedure. Instead, model selection was broken up into four steps. In each step we evaluated if subsets of parameters could be combined. 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 of beetles. Therefore, in the second step we evaluated motility in each of the spatial units of the landscape taking feeding level into account. In the third step we determined whether habitats with similar values for motility could be merged into functional units. In the fourth and last step we determined the need to distinguish habitats when assessing interface-mediated behaviour.

2.3 Prey availability in habitats

Prey availability was estimated by measuring body mass of the naturally occurring (i.e. unmarked) beetles in the different spatial units that were captured on 22 and 28 July 2010. A Kruskal-Wallis test was used to test for an effect of habitat on beetle body weight, and a post hoc test with Bonferroni correction was used to test for significant contrasts between spatial units.

3 Results

3.1 Recapture rate and dispersal distances

In total 865 of the 3665 marked beetles were recaptured within the 22 days sampling period. Of the recaptured beetles a significant proportion had crossed one (12.3%) or two (6.4%) habitat interfaces. Six beetles (0.7%) crossed three or more interfaces. The remaining 80.7% of recaptures were made within the field of release. Relatively few beetles were recaptured in field 1 compared to the other habitats (Table 1).

3.2 Model selection

In the first step we compared eight model variants of 3 to 6 parameters in which the parameters motility, relative loss rate and relative recapture rate were estimated for fed and starved beetles separately and for fed and starved beetles jointly. In these models, it was assumed that the habitat itself did not affect motility. A comparison of the models based on AIC (Table 2) indicated support from data for an effect of feeding level on motility (model 1 compared to model 4: $\Delta\text{AIC} = 2.8$) and general loss rate (model 1 compared to model 7: $\Delta\text{AIC} = 7.1$). Fed beetles had a lower motility (26.1 vs $33.3 \text{ m}^2 \text{ d}^{-1}$) and larger loss rate (0.09 vs 0.05 d^{-1}) than starved beetles (Table 2). There was no support from the data for an effect of feeding level on trapping efficiency (model 1 compared to model 2: $\Delta\text{AIC} = 1.9$).

In the next step we included the effect of habitat on motility (Table A2) and habitat preference (Table A3). This resulted in 13 model variants with a maximum of 28 parameters. Inclusion of habitat specific parameters caused a major model improvement in terms of AIC compared to the best model identified in the first step, which did not distinguish habitats ($\Delta\text{AIC} = 95$). Feeding level had a weak effect and only on motility in field 3 (Variant 3 compared to full model: $\Delta\text{AIC} = 1.7$) (Table A2). Based on these results feeding level was not further considered in the next steps of model selection.

Table 2 Model selection to assess the overall influence of feeding level on motility, relative loss rate and trapping efficiency. The order of models is determined by their AIC value. Model 1 had most support of the data. ΔAIC is the difference in AIC between model x and model 1. Parameter estimates for fed and starved beetles jointly are shown in grey.

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8
NLL	845.7	845.6	847.0	848.1	847.7	850.5	850.2	850.5
k	5	6	5	4	5	3	4	4
AIC	1701.4	1703.3	1703.9	1704.1	1705.3	1707.0	1708.4	1709.0
ΔAIC	0	1.9	2.6	2.8	4.0	5.6	7.1	7.7
μ_1 ($\text{m}^2 \text{ d}^{-1}$)	26.1	25.4	29.0	29.0	24.5	28.3	28.9	27.9
μ_2 ($\text{m}^2 \text{ d}^{-1}$)	33.3	33.4			35.3		31.1	
ξ_1 (d^{-1})	0.05	0.06	0.05	0.06	0.07	0.07	0.07	0.07
ξ_2 (d^{-1})	0.09	0.09	0.09	0.08				
ω_1 (m^{-2})	0.011	0.012	0.010	0.011	0.014	0.011	0.010	0.013
ω_2 (m^{-2})		0.011	0.013		0.008			0.011

k : number of parameters; μ_i : motility ($\text{m}^2 \text{ d}^{-1}$); ξ_i : relative loss rate (d^{-1}); ω_i : trapping-efficiency (m^{-2}).

The indices indicate the parameter value for fed ($i = 1$) and starved ($i = 2$) beetles.

In the third step we assessed whether habitats with similar parameter values for motility in step 2 could be combined without significant loss of information. We formulated three model variants in which motility parameters were combined for margins 1 and 2; fields 1, 3 and 4; and fields 2 and 5, respectively. In a fourth model variant, all combinations of the previous three models were combined. The latter model variant had most support from the data as indicated by AIC (variant 4 in Table 3). Thus, the number of habitats could be reduced from seven fields to three functional types.

Table 3 Model selection to identify functionally different habitat types. Four model variants are compared to the full model. Δ AIC indicates the difference in AIC between the model variants and the full model. Parameters estimated for multiple spatial units are shown in grey.

Spatial attribute	Parameter	Full model	Variant 1	Variant 2	Variant 3	Variant 4
	NLL	779.3	779.6	779.9	780.0	780.9
	k	16	15	15	14	12
	AIC	1590.6	1589.2	1589.8	1588.1	1585.8
	Δ AIC	0.0	-1.4	-0.9	-2.6	-4.8
Margin 1	μ ($\text{m}^2 \text{d}^{-1}$)	3.7	5.4	3.2	4.9	5.3
Margin 2	μ ($\text{m}^2 \text{d}^{-1}$)	6.6		6.4	6.4	
Field 2	μ ($\text{m}^2 \text{d}^{-1}$)	22.9	22.4	26.0	23.2	25.0
Field 5	μ ($\text{m}^2 \text{d}^{-1}$)	27.3	27.0		27.5	
Field 4	μ ($\text{m}^2 \text{d}^{-1}$)	57.1	63.7	65.5		
Field 3	μ ($\text{m}^2 \text{d}^{-1}$)	59.4	60.2	59.5	62.2	60.2
Field 1	μ ($\text{m}^2 \text{d}^{-1}$)	100.0	100.0	100.0		
Field1-Margin1	π_1 (-)	0.15	0.24	0.13	0.19	0.20
Field2-Margin1	π_2 (-)	0.10	0.10	0.10	0.11	0.11
Field2-Field3	π_3 (-)	0.45	0.47	0.44	0.44	0.47
Field3-Margin2	π_4 (-)	0.21	0.21	0.21	0.21	0.22
Field4-Margin2	π_5 (-)	0.86	0.82	0.86	0.87	0.81
Field4-Field5	π_6 (-)	1.93	2.01	1.97	2.00	1.91
global	ξ_1 (d^{-1})	0.059	0.059	0.059	0.058	0.061
global	ξ_2 (d^{-1})	0.080	0.080	0.080	0.079	0.082
global	ω (d^{-1})	0.010	0.010	0.010	0.010	0.011

k : number of parameters; μ : motility ($\text{m}^2 \text{d}^{-1}$); π : interface-mediated behaviour; ξ_i : relative loss rate for fed ($i=1$) and starved ($i=2$) beetles (d^{-1}); ω : trapping-efficiency (m^{-2}).

Table 4. Model selection to determine the support of data for interface-mediated behaviour. Δ AIC is the difference in AIC between the model variants with the full model. A negative Δ AIC indicates more support of the data for the full model, while a positive Δ AIC indicates more support for the model variant. Missing values for interface-mediated behaviour were set to 1 in model calibration.

Spatial attribute		Full model	Variant 1	Variant 2	Variant 3	Variant 4	Variant 5	Variant 6
	NLL	780.9	782.8	801.0	782.5	792.7	780.9	783.3
	k	12	11	11	11	11	11	11
	AIC	1585.8	1587.5	1624.1	1587.0	1607.4	1583.8	1588.7
	Δ AIC	0.0	1.7	38.2	1.2	21.6	-2.0	2.9
Margin 1 and 2	μ	5.3	7.4	5.6	6.7	6.3	5.8	5.9
Field 2 and 5	μ	25.0	27.0	23.5	26.6	24.1	26.1	25.6
Field 1, 3 and 4	μ	60.2	63.2	56.8	61.0	58.3	63.3	59.3
Field1-Margin1	π_1	0.20		1.77	0.33	0.26	0.22	0.21
Field2-Margin1	π_2	0.11	0.15		0.11	0.11	0.10	0.11
Field2-Field3	π_3	0.47	0.43	0.40		0.77	0.45	0.45
Field3-Margin2	π_4	0.22	0.21	0.21	0.24		0.23	0.21
Field4-Margin2	π_5	0.81	0.89	0.85	0.90	2.46		1.00
Field4-Field5	π_6	1.91	1.94	1.95	1.92	1.98	1.90	
global	ξ_1	0.061	0.058	0.058	0.061	0.060	0.058	0.061
global	ξ_2	0.082	0.079	0.081	0.081	0.082	0.079	0.081
global	ω	0.011	0.009	0.012	0.010	0.012	0.010	0.010

k : number of parameters; μ : motility ($\text{m}^2 \text{d}^{-1}$); π : interface-mediated behaviour; ξ_i : relative loss rate for fed ($i=1$) and starved ($i=2$) beetles (d^{-1}); ω : trapping-efficiency (m^{-2}).

The best model from step 3 (variant 4 in Table 3) was used as the full model in step 4 to assess the contribution to model fit of parameters describing preferences at habitat interfaces. This resulted in 6 model variants in which subsequently one of the habitat preference parameters was set to 1 while optimizing the others (Table 4).

Model variants 1, 2, 3, 4 and 6 had a greater AIC than the full model (Table 4), indicating that preference parameters for the associated interfaces should be retained in the model. Especially, preferences at the interfaces of field 2 and margin 1 (variant 2, Table 4); and field 3 and margin 2 (variant 4, Table 4) caused a large change in AIC compared to the full model, indicating strong support for these parameters. There was no support of the data for preference at the interface of field 4 and margin 2 (variant 5), as indicated by a change in AIC of less than 2 compared to the full model. Model variant 5 had the smallest AIC of all models in the procedure and was selected as the best model for describing beetle dispersal over time in our experiment.

Table 5 Comparison of parameter values of the best model optimized for the one dimensional (1D) representation of the landscape, which was used for model simplification, and for the original two dimensional (2D) landscape. For the best model in the 1D landscape the 95% confidence margins are shown between parentheses.

Spatial attribute	Parameter	1D	2D
	NLL	782.8	1438.7
Margin 1 and 2	μ ($\text{m}^2 \text{d}^{-1}$)	5.8 (3.4 – 14.0)	7.2
Field 2 and 5	μ ($\text{m}^2 \text{d}^{-1}$)	26.1 (21.0 – 33.0)	21.9
Field 1, 3 and 4	μ ($\text{m}^2 \text{d}^{-1}$)	63.3 (48.0 – 86.0)	50.2
Field1-Margin1	π_1 (-)	0.22 (0 – 1.0)	0.39
Field2-Margin1	π_2 (-)	0.10 (0.05 – 0.21)	0.13
Field2-Field3	π_3 (-)	0.45 (0.15 – 1.15)	0.47
Field3-Margin2	π_4 (-)	0.23 (0.14 – 0.4)	0.31
Field4-Field5	π_6 (-)	1.90 (1.1 – 3.3)	2.01
global	ξ_1 (d^{-1})	0.058 (0.04 – 0.076)	0.063*
global	ξ_2 (d^{-1})	0.079 (0.06 – 0.10)	
global	ω (d^{-1})	0.010 (0.007 – 0.014)	0.119

μ : motility ($\text{m}^2 \text{d}^{-1}$); π : interface-mediated behaviour; ξ_i : relative loss rate for fed ($i=1$) and starved ($i=2$) beetles (d^{-1}); ω : trapping-efficiency (m^{-2}). *Excessive calculation time necessitated simplifying the 2D model by using a global parameter for relative loss rate.

3.3 Analysis of the best model

Predictions by the best model (Table 5) of the total number of recaptured beetles at the end of the experiment fell within the confidence interval of the data for 22 of the 25 recapture distances (Fig. 2). Also the accumulation of beetles through time was well predicted by the model for most recapture distances. Confidence intervals for the parameters of the best model (see Table 5) were derived from the log-likelihood profiles (Bolker 2008) in Figure 3. The non-overlapping confidence intervals for the motility parameters of the best model show that these parameters were significantly different from each other (Fig. 3A). The confidence intervals for the habitat preference parameters π_1 and π_3 included 1, which means that these parameters could not be identified based on the data. The parameters for the crop-margin interface at the sides closest to the release lines (π_2 and π_4) were not significantly different and were most accurately estimated as revealed by the narrow confidence intervals.

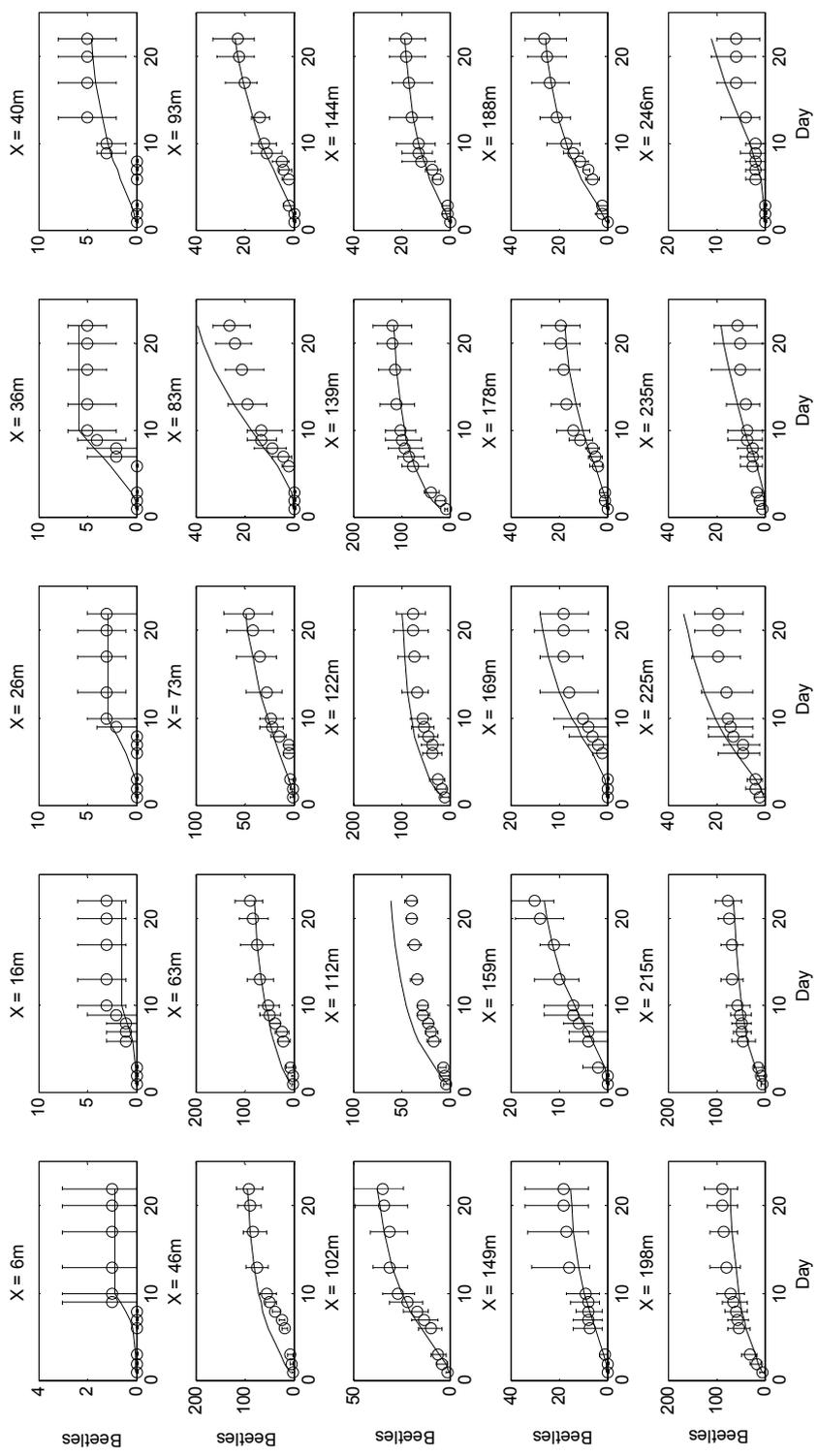


Fig. 2 Cumulative number of recaptured beetles (observed \circ ; predicted $-$) through time at each recapture point in the 1D representation of the landscape. For explanation see text. The x-coordinate of the recapture point is shown above the figure. Error-bars show the 95% confidence interval of the observations.

The confidence interval for habitat preference at the barley-mustard interface (π_5) was just above one, again indicating difficulty in accurately estimating the effect of the interface on movement.

The best model was fitted to a one dimensional representation of the landscape data. We used the same model structure and fitted this to the original two dimensional landscape data. Parameter values for motility and interface mediated behaviour were similar to those for the one dimensional model (Table 5). The one- and two dimensional models thus qualitatively described the same dispersal behaviour of ground beetles in the landscape mosaic.

3.4 Prey availability in spatial units

The mean body weight of the naturally occurring beetles that were captured on 22 July, two days after release of the marked beetles, was significantly different between spatial units (Kruskal-Wallis test: $\chi^2 = 30.1$; $df=6$; $p < 0.001$). The greatest mean body weight was found in mustard in field 5 and the lowest in barley fields 2 and 3. Body weight values in the other spatial units (field 1, field 4, margin 1 and margin 2) were intermediate and not significantly different from any of the other spatial units (Fig. 4A). Also on 28 July body weight was significantly different between spatial units (Kruskal Wallis test: $\chi^2 = 78.9$; $df=6$; $p < 0.001$). The relative differences in body weight between spatial units were similar to the pattern on 22 July but the absolute values had decreased for all habitats except fields 2 and 3 (Fig. 4B).

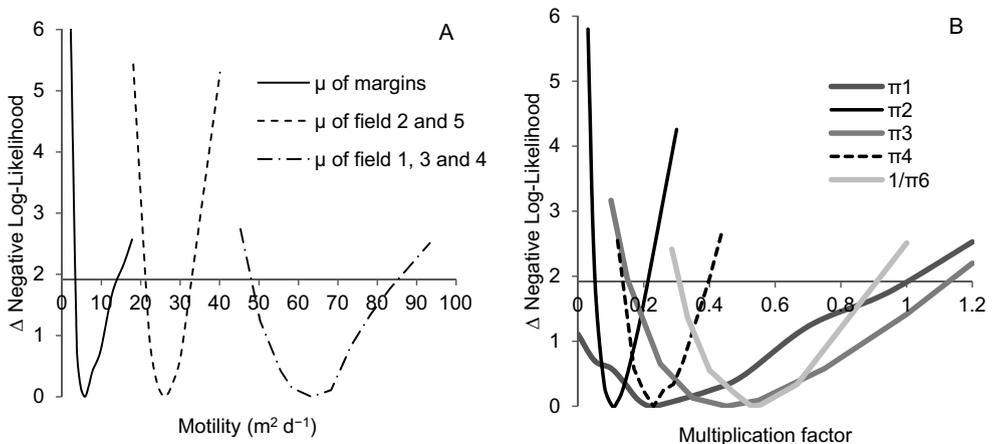


Fig. 3 Likelihood profile of the parameters for motility (A) and interface mediated behaviour (B) of the best model (Table 5). The left and right crossing of a profile with the x-axis mark the lower and upper limits, respectively, of the parameter's 95% confidence interval. The interface mediated behaviour parameter for the flux of beetles between field 4 and 5 (π_6) was inverted to scale with the other interface multiplication factors. The reciprocal of π_6 is equal to the multiplication factor for the flux of beetles from field 5 to 4.

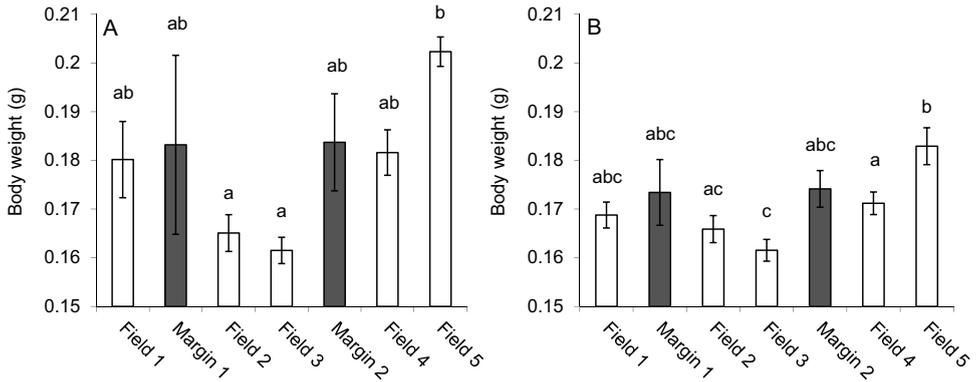


Fig. 4 Mean body weight (\pm se) of the background population of *P. melanarius* in the different spatial units of the habitat mosaic on 22 July (A) and 28 July (B). A Kruskal-Wallis test was used to test for an effect of habitat type on beetle weight, and a post hoc test with Bonferroni correction was used to test for significant contrasts between spatial units. Different letters denote significant differences in mean body weight of beetles between spatial units for a particular date. Grey bars denote the perennial field margins and white bars crop habitats. Fields 1-4 consisted of barley and field 5 consisted of mustard.

4 Discussion

In this study habitat heterogeneity was used to describe within season dispersal behaviour of the common generalist ground predator *P. melanarius*. Semi-natural grass margins were functionally different from crop habitats in terms of their effect on motility and behaviour at habitat interfaces. Motility in the margins was lower than in the crop, and at the interface movement was biased towards the crops. The crop areas could be merged into units with high or low motility. The difference in motility between these units was not related to crop species, tillage regime, or beetle weight as indicator of food availability. In this section we compare the results to the scant information in the literature on motility and habitat preference, discuss methodological issues and conclude on the importance of landscape heterogeneity for dispersal of the carabid species studied.

Feeding level of beetles at the moment of release did not play a significant role in explaining the dispersal pattern of *P. melanarius* in our landscape mosaic. Apparently, beetles responded more to local food conditions than to their feeding history. Seven days after release of starved and fed beetles, beetles from both groups had the same weight (results not shown). Fournier and Loreau (2001) found that starved *P. melanarius* were significantly

more active than satiated beetles, but this difference disappeared already after the first day as starved beetles gained weight and satiated beetles lost weight. Wallin and Ekbohm (1994) only found a difference in movement rate for starved females and only at low aphid density. To relate dispersal behaviour to the physiological state of beetles, it thus seems more important to have information on food availability in the field than to control for feeding level at the start of the experiment.

Grassy banks and hedgerows have been found to act as barriers for movement of *P. melanarius* in earlier studies (Frampton et al. 1995; Mauremooto et al. 1995; Thomas et al. 1998), which was hypothesized to be due to reduced motility in the margins, or reluctance of beetles to enter the margins (Frampton et al. 1995). Our study provides for the first time evidence that shows that both mechanisms play a role. A higher preference of *P. melanarius* for the crops compared to the margins was unexpected as semi-natural habitats have been reported to harbour more prey than crop habitats (Lewis 1969; Nentwig 1988; Bommarco 1999; Fournier and Loreau 2001). The preference of beetles for the crop habitat, however, may be due to a higher rate of food acquisition by *P. melanarius* in the crop habitat than in the grassy margin as was suggested by Fournier (2001). In our study, however, the weight of the naturally occurring beetle population was significantly higher in mustard than in some of the barley fields, and intermediate in the margins. Thus, food availability as inferred from the beetle weight did not fully explain the preference of beetles for the crop compared to the margin.

Food availability as inferred from beetle weight could also not explain differences in motility between habitats. Beetle weight is an indicator of the history of prey consumption and does not necessarily reflect actual food availability, because consumed prey are digested within days (data for *Poecilus versicolor*; Mols 1993). The movement of beetles between habitats, furthermore, makes it difficult to attribute differences in beetle weight to habitats. This could explain why we did not find a difference in beetle weight between fields 2 and 3, despite a difference in motilities. This difference in motility between fields 2 and 3 may be related to soil management practices: minimum tillage in field 2 and conventional mouldboard ploughing in field 3. Soil disturbance caused by ploughing may have reduced the soil fauna (House and Parmelee 1985; Chan 2001) and thus the prey availability for *P. melanarius* which may explain the higher motility in field 3 compared to field 2.

The values of motility that we found are similar to those previously reported for *P. melanarius* in arable land during summer (Chapter 3). The motility we found in the margins ($5.8 \text{ m}^2 \text{ d}^{-1}$) is

similar to motility approximated from movement rate of *P. melanarius* in a deciduous forest ($7.3 \text{ m}^2 \text{ d}^{-1}$) (Wallin and Ekblom 1988; Chapter 3). The two motility values for the crop habitats ($26.1 \text{ m}^2 \text{ d}^{-1}$ and $63.3 \text{ m}^2 \text{ d}^{-1}$) fall in the range of $18 - 215 \text{ m}^2 \text{ d}^{-1}$ in crop habitats reviewed in (Chapter 3). We hypothesize that the low range motility values are associated with favourable conditions resulting in random movement and short movement distances, while the high range records are associated with unfavourable conditions leading to directed movements and large movement distances (Baars 1979).

The habitat preference parameters can be expressed as a probability to move from one side of an interface to the other. The average preference parameter for the two crop-margin interfaces (field 2-margin and field 3-margin) translates to a probability of 0.83 to move to barley and 0.17 to move to the margin. The preference parameter for the barley-mustard interface (field 4-field 5) translates to a probability of 0.34 to move to barley and 0.66 to move to mustard. Similar probabilities were found for an oilseed-radish – rye interface, which were 0.40 and 0.60 for movement towards rye and oilseed-radish, respectively (Chapter 3).

We encountered a number of methodological problems. Obtaining precise estimates for both movement rates and habitat preferences was difficult as these parameters can compensate each other during estimation (Ovaskainen et al. 2008b). In our study, habitat preferences at the field 1-margin 1 and field 2-field 3 interface could not be demonstrated, as shown by confidence intervals for these parameters, which included 1. The habitat preference for the field 4-margin 2 interface was equal to 1. The grass margins had two interfaces with a crop. The number of beetles reaching the closer crop-margin interface after being released was higher than the number of beetles reaching the farther interface. There was thus more data to estimate the habitat preference for the closer than for the farther interface. Estimation would be improved when beetles are released at equal distances from interfaces (see Chapter 4). Motility in field 1 could not reliably be estimated (Table 3) due to low recapture rates (Table 1). This problem could be solved by releasing beetles in field 1. These solutions, however, increase the already substantial effort involved in this type of mark-recapture experiments.

If we assume that motility of beetles is constant during a growing season, the range of population spread of *P. melanarius* is between 3.2 and 7.7 ha after 14 weeks depending on motility in the crop habitats (26 or $63 \text{ m}^2 \text{ d}^{-1}$, Table 5). 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 field tracking. The average dispersal distance associated with these

areas, calculated as radii of circles, is between 100 and 160 m. For a landscape with an average field size of 100 by 100 m we expect little redistribution of *P. melanarius* between fields, even more when fields are surrounded by grass margins or hedgerows. Since *P. melanarius* reproduces and overwinters in crop habitats, we expect next year's biological control potential by this predator to be more dependent on local field management than on compositional heterogeneity of the landscape mosaic surrounding a field. The next challenge in research on dispersal of arthropods is to see if model prediction based on data collected in one year and landscape are also valid for other years and landscapes.

Acknowledgments

We wish to thank Dine Volker for technical support during the experiments. Special thanks go to Delphine Costomiris, Anaïs Augé and Jay Jivan Kessaodjee, who contributed to this work through their Msc internship research. This project was financially supported by strategic research funds of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation and was part of the strategic research program "Sustainable spatial development of ecosystems, landscapes, seas and regions" which was funded by the Dutch Ministry of Agriculture, Nature Conservation and Food Quality, and carried out by Wageningen University and Research centre (KB-01-008-024-ALT).

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Appendix

Table A1 Overview of dispersal behaviour of carabid beetles across heterogeneous habitats in agro-ecosystems.

Reference	Species	Land uses	Main result
Wallin and Ekborn (1988)	<i>Pterostichus melanarius</i> ,	cereals, mixed deciduous	Lower movement speed (m h^{-1}) in wood than in cereals
	<i>Pterostichus niger</i>	wood	
Duelli et al. (1990)	Carabidae spp.	cereal, maize, semi-natural	Almost all identified carabid species crossed field borders. Especially at a maize-wheat interface there was a large difference between the numbers of beetles moving in each direction. More beetles arrived at the interface coming from wheat than beetles coming from maize.
		habitat	
Lys et al. (1991)	<i>Pterostichus melanarius</i> ,	Wheat field during crop	For <i>P. melanarius</i> and <i>H. rufipes</i> an increase in surface activity was found after field operations. For <i>P. melanarius</i> and <i>P. cupreus</i> an increase in surface activity was also found during their reproductive period which was not induced by farming operations.
	<i>Pterostichus anthracinus</i>	growth, wheat field after	
	<i>Harpalus rufipes</i>	harvesting, wheat field after	
	<i>Pterostichus niger</i>	tillage,	
	<i>Poecilus cupreus</i>		
Lys et al. (1992)	<i>Pterostichus melanarius</i> ,	Wheat field during crop	More individuals of <i>P. cupreus</i> and <i>P. melanarius</i> moved from the wheat field without strips to the strip-managed areas than vice versa. <i>Carabus granulatus</i> mainly kept to the cereal areas. After harvest only <i>P. niger</i> and <i>H. rufipes</i> distinctly preferred the strips.
	<i>Poecilus cupreus</i> ,	growth, wheat field after	
	<i>Carabus granulatus</i>	harvest, wheat field	
Kennedy (1994)	<i>Carabus nemoralis</i>	intersected by perennial strips (strip-managed area)	Dispersal speed increased with land use intensification (semi-natural < set-aside < arable areas)
		arable, set aside and semi-natural areas	
Wallin and Ekborn (1994)	<i>Pterostichus melanarius</i> ,	cereals	Net displacement was lowest at highest aphid density.
	<i>Pterostichus niger</i> ,		
	<i>Poecilus cupreus</i>		

Table A1 continued

Reference	Species	Land uses	Main result
Frampton et al. (1995)	<i>Pterostichus melanarius</i> , <i>Pterostichus niger</i> , <i>Harpalus rufipes</i>	cereal, grassy bank	Movement of all species was slower through a grassy bank than through a barley crop. The time between release and recaptures of starved and fed <i>P. melanarius</i> and <i>H. rufipes</i> was increased by the presence of the grassy bank.
Mauremooto et al. (1995)	<i>Harpalus rufipes</i> , <i>Pterostichus melanarius</i> , <i>Pterostichus madidus</i>	barley, hedgerow	For all species movement was markedly slowed in the hedgerow compared with the barley field. Starvation prior to release resulted in a more rapid crossing of the boundary, especially for <i>P. melanarius</i> (both sexes) and <i>H. rufipes</i> females
Zhang et al. (1997)	<i>Harpalus rufipes</i>	potato, cereal	No difference in dispersal distance after one day between crop species.
Thomas et al. (1998)	<i>Pterostichus melanarius</i>	cereal, hedgerow	Approximately 5.75% of recaptures were from releases on the opposite side of the hedgerow, whereas for the movement parallel to the hedgerow the percentage of recaptures was approximately 20%.
García et al. (2000)	<i>Nebria brevicollis</i>	recently harvested cereal field, hedgerow	There was considerable movement within fields but the hedgerow was a significant barrier to dispersal between fields.
Martin et al. (2001)	<i>Abax ater</i>	cereal, corn, wood, hedgerow	Flows of individuals from hedgerows to fields were low, whereas many individuals released in woods were recaptured in cornfields.
Bommarco and Fagan (2002)	<i>Poecilus cupreus</i>	cereal, ley	Early in the season <i>P. cupreus</i> appeared 'attracted' to ley in the vicinity of a ley-barley interface. Diffusion rates were consistently higher in barley than in ley early in the season, while late in the season the opposite was found. These patterns were attributed to variation in prey availability.

Table A1 continued

Reference	Species	Land uses	Main result
Holland et al. (2004)	<i>Pterostichus melanarius</i> , <i>Pterostichus madidus</i>	arable matrix (cereal fields intersected by hedgerows)	Movement out of the original release block was least when activity-density of the naturally occurring population was highest.
Kujawa et al. (2006)	<i>Harpalus rufipes</i>	cereals, corn shelterbelt	There was more movement of <i>H. rufipes</i> from a shelter-belt to the crop field (cereal or corn) than in the opposite direction
Thomas et al. (2006)	<i>Pterostichus melanarius</i>	wheat, beans	Activity and mean smallest displacement distance was larger in beans compared to wheat, which the authors attributed to lower plant density in beans.
Chapter 4 this thesis	<i>Pterostichus melanarius</i>	oilseed-radish, rye	No difference in motility between crop species. Beetles moved more frequently from rye into oilseed radish than vice versa which was attributed to a 1.5 greater preference of beetles for oilseed radish than for rye when located at the interface.

Table A2 Model selection to determine the effect of feeding level on motility. Model selection to determine the effect of feeding level on motility and interface-mediated behaviour. The effect of feeding level was assessed by comparing the full model with model variants in which parameters for fed and starved beetles were jointly estimated (shown in grey). The second column indicates the subject to which the parameter applies, either a single habitat (e.g. Field 1) or a habitat interface (e.g. Field 1 – Margin 1). ΔAIC is for the difference in AIC between the model variants with the full model. A negative ΔAIC indicates more support of the data for the model variant, while a positive ΔAIC indicates more support for the full model. Models for which $|\Delta AIC| < 2$ are considered equivalent. Upper values in the parameter rows are for fed beetles; lower values for starved beetles. If motility was calibrated for both fed and starved beetles the value is shown in the centre.

Spatial attribute	Parameter	Full model	Variant 1	Variant 2	Variant 3	Variant 4	Variant 5	Variant 6	Variant 7
	NLL	774.2	774.2	774.5	776.0	774.3	774.3	774.4	774.3
	AIC	1606.4	1604.5	1604.9	1608.1	1604.6	1604.6	1604.9	1604.6
	ΔAIC	0	-1.9	-1.5	1.7	-1.7	-1.8	-1.5	-1.8
Field 1	μ_1	90.1	99.6	98.9	98.2	95.3	99.3	92.7	93.3
	μ_2	98.6		99.6	100.0	99.6	99.7	98.9	95.4
Field 2	μ_1	22.2	20.8	22.6	21.3	21.3	21.5	21.9	20.7
	μ_2	25.5	25.1		26.2	24.7	25.3	26.1	24.7
Field 3	μ_1	48.0	45.5	45.5	60.9	46.2	46.1	46.9	45.8
	μ_2	80.7	76.8	77.8		77.1	78.2	80.2	75.1
Field 4	μ_1	44.5	41.0	45.4	45.7	49.3	41.0	45.7	47.5
	μ_2	63.6	62.8	59.3	63.9		65.6	70.6	59.6
Field 5	μ_1	27.9	26.9	27.0	27.5	26.5	28.3	28.0	26.2
	μ_2	30.1	28.4	28.6	29.3	28.8		29.4	27.5
Margin 1	μ_1	3.5	3.1	3.2	3.4	3.0	2.7	4.3	2.8
	μ_2	4.3	4.0	4.6	4.3	4.3	4.5		4.1

Margin 2	μ_1	9.5	8.4	8.2	7.0	8.5	8.6	9.4	6.9
	μ_2	6.7	5.9	6.3	7.8	6.6	5.7	6.2	
Field 1 –	π_1	0.24	0.12	0.20	0.17	0.13	0.11	0.24	0.10
Margin 1	π_2	0.21	0.18	0.19	0.18	0.20	0.23	0.19	0.18
Field 2 –	π_1	0.07	0.06	0.06	0.07	0.07	0.07	0.07	0.06
Margin 1	π_2	0.17	0.17	0.17	0.16	0.17	0.17	0.17	0.17
Field 2 –	π_1	0.67	0.77	0.76	0.67	0.73	0.69	0.70	0.73
Field 3	π_2	0.21	0.24	0.22	0.20	0.23	0.24	0.22	0.23
Field 3 –	π_1	0.22	0.23	0.23	0.22	0.23	0.23	0.23	0.23
Margin 2	π_2	0.19	0.20	0.19	0.19	0.23	0.20	0.20	0.20
Field 4 –	π_1	1.02	1.04	1.03	1.02	1.07	1.04	1.09	1.01
Margin 2	π_2	0.74	0.76	0.66	0.70	0.81	0.70	0.79	0.78
Field 4 –	π_1	1.21	1.16	1.19	1.23	1.31	1.15	1.26	1.29
Field 5	π_2	2.51	2.39	2.45	2.51	2.24	2.49	2.52	2.50
global	ξ_1	0.054	0.058	0.059	0.056	0.058	0.057	0.055	0.057
	ξ_2	0.079	0.082	0.080	0.080	0.082	0.081	0.079	0.082
global	ω	0.009	0.011	0.010	0.010	0.011	0.010	0.010	0.011

μ_i : motility ($m^2 d^{-1}$); π : interface-mediated behaviour; ξ_j : relative loss rate (d^{-1}); ω_j : trapping-efficiency (m^{-2}). The indices indicate the parameter value for fed ($i=1$) and starved ($i=2$) beetles.

Table A3 Model selection to determine the effect of feeding level on interface-mediated behaviour. Model selection to determine the effect of feeding level on motility and interface-mediated behaviour. The effect of feeding level was assessed by comparing the full model with model variants in which parameters for fed and starved beetles were jointly estimated (shown in grey). The second column indicates the subject to which the parameter applies, either a single habitat (e.g. Field 1) or a habitat interface (e.g. Field 1 – Margin 1). ΔAIC is for the difference in AIC between the model variants with the full model. A negative ΔAIC indicates more support of the data for the model variant, while a positive ΔAIC indicates more support for the full model. Models for which $|\Delta AIC| < 2$ are considered equivalent. Upper values in the parameter rows are for fed beetles; lower values for starved beetles. If motility was calibrated for both fed and starved beetles the value is shown in the centre.

Spatial attribute	Parameter	Full model	Variant 8	Variant 9	Variant 10	Variant 11	Variant 12	Variant 13
	NLL	774.2	774.2	775.0	774.9	774.3	774.3	774.7
	AIC	1606.4	1604.5	1606.1	1605.9	1604.6	1604.6	1605.4
	ΔAIC	0	-1.9	-0.3	-0.5	-1.8	-1.7	-0.9
Field 1	μ_1	90.1	98.7	79.4	93.6	96.8	98.4	92.1
	μ_2	98.6	99.5	99.8	95.8	99.7	98.1	98.9
Field 2	μ_1	22.2	21.0	21.8	22.0	20.9	21.5	21.2
	μ_2	25.5	24.4	25.6	25.8	24.6	25.4	24.7
Field 3	μ_1	48.0	46.9	47.0	47.9	47.3	47.8	46.4
	μ_2	80.7	76.3	78.4	81.0	76.5	79.8	79.0
Field 4	μ_1	44.5	42.3	42.7	46.5	40.9	42.1	60.4
	μ_2	63.6	57.7	57.6	64.9	57.8	65.5	49.1
Field 5	μ_1	27.9	26.8	27.1	27.0	26.7	27.2	25.9
	μ_2	30.1	28.4	29.4	29.8	28.3	29.0	28.6
Margin 1	μ_1	3.5	3.3	3.0	2.7	3.3	3.2	3.4
	μ_2	4.3	4.4	4.9	5.1	4.6	4.4	4.5

Margin 2	μ_1	9.5	8.1	8.6	8.4	8.4	8.4	7.6
	μ_2	6.7	6.1	6.2	5.8	6.3	6.1	6.1
Field 1 – Margin 1	π_1	0.24	0.19	0.23	0.11	0.15	0.15	0.17
	π_2	0.21		0.14	0.21	0.22	0.21	0.21
Field 2 – Margin 1	π_1	0.07	0.07	0.11	0.07	0.07	0.07	0.07
	π_2	0.17	0.16		0.16	0.16	0.16	0.16
Field 2 – Field 3	π_1	0.67	0.72	0.72	0.42	0.73	0.72	0.70
	π_2	0.21	0.23	0.24		0.23	0.22	0.23
Field 3 – Margin 2	π_1	0.22	0.22	0.23	0.22	0.22	0.22	0.22
	π_2	0.19	0.20	0.20	0.22	0.22	0.21	0.21
Field 4 – Margin 2	π_1	1.02	0.99	1.05	1.09	0.99	0.90	0.92
	π_2	0.74	0.77	0.72	0.74	0.79		0.76
Field 4 – Field 5	π_1	1.21	1.21	1.19	1.30	1.17	1.28	1.94
	π_2	2.51	2.38	2.41	2.61	2.34	2.47	
global	ξ_1	0.054	0.057	0.056	0.054	0.056	0.056	0.056
	ξ_2	0.079	0.081	0.082	0.082	0.081	0.080	0.082
global	ω	0.009	0.010	0.010	0.010	0.010	0.010	0.010

μ_i : motility ($m^2 d^{-1}$); π_i : interface-mediated behaviour; ξ_i : relative loss rate (d^{-1}); ω : trapping-efficiency (m^{-2}). The indices indicate the parameter value for fed ($i=1$) and starved ($i=2$) beetles.

Chapter 6

General discussion

1 Introduction

Recognition of the threats posed by the use of pesticides to human health and the environment has urged the European Commission to set goals to develop an agricultural industry that is less dependent on synthetic pesticides (Directive 2009/128/EC). Conservation biological control is one of the strategies in integrated pest management that can help reduce dependency of farmers on pesticides by providing natural control of pests by entomophagous arthropods. The success of conservation biological control depends on knowledge about the resources these natural enemies need and how they distribute themselves over the landscape. Insight into how movement influences in-field populations and the associated biocontrol services is limited by a lack of quantitative data on movement processes and a lack of standardization in the quantification of dispersal behaviour (Schellhorn et al. 2014). The aim of this thesis was to quantify movement and dispersal behaviour of the carabid predator *P. melanarius* according to a standard movement model and to understand how dispersal of this species is affected by landscape heterogeneity. In this chapter I discuss the results presented in the experimental chapters and offer ideas for further research.

2 Insight into movement of *Pterostichus melanarius*

2.1 Influence of light on nocturnal movement behaviour

Carabid beetles are, like many insects, assumed to be insensitive to red light. However, my observation that the behaviour of beetles was different under red light compared to a near infrared radiation (nir) source indicates that beetles are sensitive to red light (Chapter 2). Compared to nir, white light resulted in a stronger behavioural change than red light. These results indicate that behaviour of a nocturnal carabid beetle is affected by light colour and/or light intensity. How light colour and light intensity affect night behaviour is relevant to research on the effect of urban light pollution on insect communities (Longcore and Rich 2004). The way in which light intensity affects night behaviour is also relevant to studies on insect behaviour under natural conditions. The observation of a night active carabid beetles moving in the same direction for several nights (Baars 1979) suggests a form of orientation in which moon or star light may play a role similar to what was found for dung beetles (Dacke et al. 2003, Dacke et al. 2013). For the study of behaviour of nocturnal carabid beetles I advise to use light conditions that are similar to the light conditions in the field, or to use nir radiation to mimic complete darkness.

2.2 Quantifying dispersal in a heterogeneous landscape

Dispersal of organisms can be measured at the individual and at the population level. Measurements at the individual level include recording movement paths, while measurements at the population level capture population redistribution patterns. In any case it is desirable that dispersal is quantified according to a common movement framework. Diffusion models provide such a framework by capturing individual movement behaviour as well as the rate of population spread with a single parameter called motility (Turchin 1998). Motility is difficult to interpret, but obtains more meaning if we know that two times the square root of motility is a measure for the expected net displacement of an individual, expressed in $m d^{-\frac{1}{2}}$. The net displacement is a less ambiguous parameter for dispersal rate than dispersal rate expressed as velocity in $m d^{-1}$ (Chapter 3). The latter assumes a linear increase in dispersal distance with time, however, dispersal distance, as a result of random movement increases with the square root of time. Although motility summarizes behaviour in one parameter it was found to be realistic enough to describe population spread of *P. melanarius* in a homogeneous crop habitat (Chapter 3). To describe population spread in a heterogeneous environment, the preference of beetles at habitat interfaces had to be accounted for (Chapter 4). Preference at an interface was simulated by a multiplication factor for the flux of beetles over the interface, which can be translated into a probability for an individual to cross an interface when situated at that interface (Chapter 4). When applied to a heterogeneous micro-landscape, a diffusion model with habitat specific motility and preference at interfaces accurately described the population spread of *P. melanarius* (Chapter 5).

Motility of *P. melanarius* was four to ten times lower in perennial grass margins compared to annual crop habitat (Chapter 5). This behavioural pattern was consistent with the pattern found in a meta-analysis for other carabid species (Chapter 3). In the meta-analysis motility of carabids was on average three times lower in a wood/hedgerow habitat compared to motility in arable land. Within arable land the meta-analysis showed a large variation of motility (Chapter 3), which may be attributed to differences in prey availability. In my own experiments the highest motility was found in the crop habitat in which I expected the lowest prey availability (oilseed radish and rye in autumn, Chapter 4), and the lowest motility was found in a crop habitat with high expected food availability (triticale/grass clover, Chapter 3). However, I was not able to identify a consistent relation between beetle weight as an indicator for prey availability and motility among habitat types in the mosaic field experiment (Chapter 5).

3 Landscape heterogeneity and carabid beetle population distribution

Landscape heterogeneity may affect carabids in two ways. At spatial scales greater than about 1 square kilometre, landscape heterogeneity affects genetic population structure (Sander et al. 2006) and at smaller spatial scales, landscape heterogeneity affects redistribution of a population between fields. The scale at which population redistribution takes place can be predicted from the motility values measured in this thesis. Using the motility estimated for crop habitat in the mosaic experiment and assuming motility to be constant during a growing season, the scale at which population redistribution takes place is in the order of magnitude of 100 – 160 m. Under Dutch conditions with fields of about 2 ha, redistribution is thus concentrated in an area encompassing a few fields and the interstitial habitat. Hedgerows or grass margins may decrease this range as they act as barriers for dispersal for at least part of the year (Chapter 5). Also, roads (Mader 1984) and water bodies can be expected to restrict the dispersal range of a population.

Whether dispersal can actually explain patterns of activity density, as found in studies such as Thomas et al. (2001), Holland et al. (2005) and Thomas et al. (2006), remains a question. Patterns of activity density have been correlated with prey density (Holland et al. 2004), soil moisture (Holland et al. 2007), vegetation density (Thomas et al. 2006) and with herbaceous or woody field boundaries (Holland et al. 2005). The contribution of dispersal in creating these patterns in activity density has received little attention so far (Schellhorn et al. 2014).

Previous studies showed asymmetries in population exchange of beetles between habitats (Duelli et al. 1990, Thomas et al. 2006), but information which would enable one to make predictions on these exchange asymmetries between different types of habitat is lacking (Rand et al. 2006). In this thesis information on population exchange between adjacent habitats was obtained by distinguishing between population exchange driven by motility and by interface mediated behaviour. For the population exchange between crop habitat and semi-natural grass margins the magnitude of the bias at the interface seemed to be related to motility in the crop habitat. The multiplication factor for motility at the crop-margin interface increased with the same factor as motility in the crop habitat for two of the three interfaces (Chapter 5). This means that the permeability of the grass margins seems to increase with increasing motility in the field. For movement at the mustard-barley (crop-crop) interface the preference was directed towards the habitat with the lowest motility, also indicating in this case, that high motility resulted in a high preference to leave.

The direction and magnitude of exchange is not only determined by motility and behaviour at habitat interfaces but also by differences in population density between habitats (Fig. 2, Chapter 4). Local population density may vary as the result of different local reproduction rates or overwintering densities. For field-inhabiting carabids such as *P. melanarius*, the observed overwintering densities in the field ranged from 8 beetles per square metre (Andersen 1997) to 106 beetles per square metre (Holland et al. 2007). Motility of field-inhabiting species ranges from 3 to 347 m² d⁻¹ (Chapter 3) and habitat preference, for *P. melanarius*, ranges from 1.5 (Chapter 4) to 10 (Chapter 5). Separating the contribution of landscape scale (dispersal) processes and local-scale (reproduction/overwintering) processes can help better understand their relative importance for population dynamics and their implications for pest suppression (Schellhorn et al. 2008). Because these processes are difficult to separate in a field setting, simulation studies are often used. Benjamin et al. (2008) simulated dispersal and local population dynamics of *P. melanarius* in realistic landscape settings and concluded that local demography was more important for population vitality than dispersal. Whether local demography was also more important for explaining patterns in population density than dispersal was not mentioned. For habitats of small size such as field margins, dispersal behaviour is more likely to explain population density patterns than for large habitats such as arable fields (Corbett and Plant 1993). In the mosaic experiment in Chapter 5 the population densities of the naturally occurring beetles in the semi-natural field margins, for example, were close to the expected equilibrium population densities, while this was not the case for population densities in the crop habitats (results not shown).

4 Implications and future research

4.1 Implications for other studies

The behavioural response of *P. melanarius* to light quality indicates that for the simulation of total darkness in the study of carabids, a nir radiation source seems most appropriate. However, total darkness is rare in the field such that red light may still be of use when observing natural night-time behaviour with both an ecological and practical relevance. The effect of red observation light on movement may have consequences for the interpretation of previous behavioural studies on nocturnal carabids and testing of red light sensitivity should therefore be undertaken for other carabid species.

In this study we quantified dispersal behaviour of a ground predator based on dispersal behaviour within and between habitats. We showed that dispersal across habitat boundaries is governed by a difference in motility between habitats and preferences at habitat interfaces.

This insight serves to provide mechanistic understanding of dispersal across habitat interfaces. This understanding might be applicable to previous simulation studies such as Westerberg et al. (2005), Sherratt and Jepson (1993) and Benjamin et al. (2008) and to empirical studies such as Macfadyen and Muller (2013) and Duelli et al. (1990). The parameterization of Westerberg's model was based on movement observations made in a homogeneous environment, and hence behaviour at a habitat interface was not accounted for. Including behaviour at habitat interfaces provides more realism to the study of carabid dispersal in heterogeneous environments.

4.2 Recommendations for future research

In this thesis I focused on the quantification of dispersal behaviour of a carabid beetle in a realistic micro-landscape setting. I showed how dispersal parameters for motility and preference at habitat interfaces can be estimated from mark-recapture data. Future studies should look into more detail on the causes of differences in motility between habitats and between studies by comparing dispersal behaviour and habitat properties simultaneously in replicated field trails. These studies should be accompanied by tracking individual movement paths because these data will provide insight into how individuals respond to differences in habitat quality, e.g. by switching from a random type of walk to a directed walk (Baars 1979). Recent advances in tracking of ground walking insects using RFID-tags may help to collect this information (Vinatier et al. 2010).

Behaviour at a habitat interface was quantified by a multiplication factor for the diffusion rate at the interface. So far we have little information on the factors that affect this parameter. An important question to address is whether edge behaviour is determined by properties of the two adjacent habitats (e.g. differences in habitat quality (Ovaskainen et al. 2008)) or whether it is determined by the interface itself (e.g. hard or soft edges (Duelli et al. 1990)).

I focused on the spatial dimension of landscape heterogeneity and did not consider changes in habitat through time, i.e. the temporal dimension. Changes of habitat (quality) as the result of disturbances such as weeding, pesticide treatment and harvest have an immediate effect on arthropod populations in the field, but little is known about the impact of these effects on their dispersal behaviour (Schellhorn et al. 2008).

Measuring dispersal behaviour is a tedious job and would require much research effort if it was to be determined for all species within a landscape. Dispersal behaviour characterized at the level of guilds of entomophagous arthropods may overcome this obstacle. With

respect to motility generalist predatory carabid beetles may for example be grouped within a single guild (Chapter 3).

The final challenge for this type of work is to translate insights into dispersal behaviour of arthropods into landscape management measures that support the redesign of landscapes to maximize the ecosystem services from conservation biological control. This requires the integration of a dynamic model of population spread with tools such as LandscapeIMAGES (Groot et al. 2010) that enable multi-objective assessments of alternative landscape configurations and reveal trade-offs between landscape functions.

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Summary

Pesticides are a major cause of environmental pollution by agriculture and a threat to human health. Biological control provided by entomophagous arthropods is one of the measures in integrated pest management that can help to reduce pesticide use. The success of biological control depends on knowledge about the resources these natural enemies need and how they distribute themselves over the landscape. The distribution of entomophagous arthropods over crop fields is affected by their dispersal capacity and landscape heterogeneity, i.e. the composition and spatial arrangement of land use. Current knowledge on entomophagous arthropod distribution and movement patterns, in particular for soil inhabiting predators, is insufficient to provide advice on how a production landscape should be re-arranged to maximally benefit from the biological control service provided by these natural enemies of agricultural pests. In particular, insight into how movement influences in-field populations and the associated biological control services is limited by a lack of quantitative data on movement across habitat interfaces and a lack of standardization in the quantification of dispersal behaviour.

This study contributes to insight into dispersal behaviour of predatory insects in an agricultural landscape as a knowledge basis for redesign of landscapes for natural pest control. The carabid beetle *Pterostichus melanarius* (Illiger) was used as model species. Dispersal behaviour of this species was studied with video equipment in experimental arenas and with mark-recapture in the field. Interpretation of the results was supported by diffusion models that accounted for habitat specific motility μ ($L^2 T^{-1}$), a measure for diffusion of a population in space and time, and preference behaviour at habitat interfaces. *Pterostichus melanarius* is a characteristic inhabitant of arable fields in Europe, which mainly moves by walking rather than flight. Overwintering and reproduction takes place in arable fields as well in semi-natural habitat. *Pterostichus melanarius* is for 90% carnivorous and eats a broad range of epigeal invertebrates, including at least fourteen agricultural pest species.

This thesis consists of an introduction, four experimental chapters and a synthesis. In Chapter 2 an experimental setup was developed for behavioural observations on movement behaviour with special attention for the effect of observation light on movement behaviour. The behavioural observations in arenas indicated that red light significantly reduced movement speed in females similar to the effect of white light and different from near infrared radiation (nir). Movement activity and pause length were also affected by radiation source, with a significant difference between nir and white light, and with intermediate values in red

light. These results indicate that *P. melanarius* has different movement behaviour under the three radiation sources, suggesting that nir rather than red radiation is most appropriate for measuring behaviour in total darkness.

Chapter 3 presents a meta-analysis on data of movement rate of carabid species collected from literature and converted to motility. The meta-analysis showed that motility of carabid spp. in farmland is three times the motility in forested land. The meta-analysis did not show consistent differences in motility between species, and a grouping of species according to gender and size did not demonstrate a significant effect of these factors. In the second part of the chapter a mark-release recapture experiment is presented with *P. melanarius* in a single field of winter triticale (*Triticosecale* Wittmack.). Motility was derived by calibrating a Fokker-Planck diffusion model to the data. The result of this calibration was similar to motility calculated from squared displacement distance and the time duration between release and recapture. The similarity between these two methods strengthens the confidence in model calibration as a suitable concept to derive motility from mark-recapture data.

In chapter 4 the influence of a crop interface on dispersal of *P. melanarius* is being investigated. A mark-recapture experiment was conducted in two adjacent fields of oilseed radish (*Raphanus sativus*) and rye (*Secale cereale*). Different diffusion models that that included, or did not include the effect of the interface were calibrated to the data with the method of chapter 3. Model selection was used to determine if behaviour at the interface was important or not. The field study was complemented by a study of movement behaviour in experimental arenas using the observation system presented in Chapter 2. Movement in the field was satisfactorily described by a Fokker-Planck diffusion model with equal motility in the two crops, and preference for oilseed radish over rye at the interface between the two crops. Beetles moved 1.5 times more frequently from rye into oilseed radish than vice versa. The values of motility in the arena were, when scaled up to field level, close to the values obtained from the field. The arena data indicated greater frequency of habitat entry into oilseed radish as compared to rye. Thus, the studies at the smaller and larger scales gave qualitatively and quantitatively similar results.

Chapter 5 describes the influence of habitat composition and configuration on within-season dispersal behaviour of *P. melanarius*. A mark-recapture experiment was conducted in an agricultural landscape mosaic consisting of perennial strips and different crop species with distinct tillage management. Food availability was assessed per habitat from the weight of naturally occurring beetles. Model selection in a set of diffusion models that included motility,

interface-mediated behaviour and beetle loss was used to identify functionally different habitat units. Semi-natural grass margins were functionally different from the crop habitats. In the margins motility was lower than in the crop habitats, and at the crop-margin interface more beetles moved towards the crop than to the margin, meaning that margins acted as barriers for dispersal. In the crop habitats motility differed between fields but no consistent relations were found with tillage or with beetle weight as an indicator of food availability. Based on the motility in crop habitats I predicted *P. melanarius* to disperse over a distance of about 100 – 160 m during a growing season in a landscape without semi-natural elements. Given this range I expect little redistribution of beetles between fields within a growing season, even more when fields are surrounded by grass margins or hedgerows. For a field of 100x100 m there will thus be little dispersal of beetles from the environment to crop fields meaning that the success of biological control by this species is more dependent on field management affecting local population dynamics than on habitat heterogeneity.

Chapter 6 presents a synthesis of the preceding chapters and discusses dispersal behaviour of carabids in relation to landscape heterogeneity. Special attention is given to the process of population exchange between habitats. For the population exchange between crop habitat and semi-natural grass margins the magnitude of the bias at the interface seemed to be related to motility in the crop habitat. The multiplication factor for motility at the crop-margin interface increased with the same factor as motility in the crop habitat for two of the three interfaces. This means that the permeability of the grass margins seems to increase with increasing motility in the field. For movement at the mustard-barley (crop-crop) interface the preference was directed towards the habitat with the lowest motility, indicating that also in this case a high motility resulted in a high preference to leave.

In this study dispersal of a ground predator was quantified based on motility within a habitat and preference behaviour at habitat interfaces during the growing season. I showed that there can be differences in motility between crop habitats and that beetles can have a preference at crop interfaces. Differences in motility as well as preference at habitat interfaces were probably related to food availability. This could be further investigated by comparing dispersal behaviour with environmental factors in replicated field trails and for different times during the year.

This thesis has resulted in a methodological approach to quantify dispersal behaviour of insects in heterogeneous environments from mark-recapture data and model calibration. The combination of models and data may lead to the development of predictive dynamic models

for population spread of entomophagous arthropods. The final step is to integrate these models with tools in which alternative landscape configurations are weighed against multiple landscape functions. In this way a spatial arrangement of landuse can be found that maximises the ecosystem service of biological pest control within a wider set of landscape functions.

Samenvatting

Pesticiden zijn een grote bron van milieuvuiling die door landbouw wordt veroorzaakt en zijn een bedreiging voor de menselijke gezondheid. Biologische bestrijding door insectenetende arthropoden is één van de maatregelen in geïntegreerde gewasbescherming dat kan helpen pesticiden te verminderen. Voor een succesvolle biologische bestrijding is kennis nodig over de hulpbronnen die deze natuurlijke vijanden nodig hebben en hoe ze zich over het landschap verspreiden. De verspreiding van insectenetende arthropoden wordt beïnvloed door hun dispersievermogen en landschapsheterogeniteit; de compositie en ruimtelijke arrangement van landgebruik. Huidige kennis over de ruimtelijke verspreiding en dispersie van insectenetende arthropoden, voornamelijk van op de bodem levende predatoren, is onvoldoende om advies te geven over hoe een productielandschap moet worden heringericht om maximaal te profiteren van de biologische bestrijding door deze natuurlijke vijanden van landbouwplagen. Er is vooral een gebrek aan kennis van dispersie over habitatgrenzen en er is een gebrek aan standaardisering in het kwantificeren van dispersiegedrag.

Deze studie draagt bij aan de ontwikkeling van methodiek voor het meten aan dispersie en aan inzicht in dispersiegedrag van op de bodem levende loopkever predator *Pterostichus melanarius* (Illiger). Dispersiegedrag van deze soort werd bestudeerd met video apparatuur in experimentele arena's en met merk-terugvang proeven in het veld. De interpretatie van de resultaten werd ondersteund door diffusiemodellen die rekening houden met habitat specifieke motiliteit μ ($L^2 T^{-1}$), een maat voor diffusie van een populatie in ruimte en tijd, voorkeursgedrag op habitatgrenzen en verlies van kevers. *Pterostichus melanarius* is een kenmerkende bewoner van akkers in Europa. Overwintering en voorplanting vindt plaats in akkers alsook in semi-natuurlijk habitat. *Pterostichus melanarius* is voor 90% carnivoor en eet een grote schare aan op de grond levende invertebraten, waaronder minstens veertien soorten landbouwplagen.

Dit proefschrift bevat een introductie, vier experimentele hoofdstukken en een synthese. Hoofdstuk 2 presenteert een experimentele setup voor observaties aan loopgedrag met speciale aandacht voor de effecten van observatielicht op loopgedrag. De gedragsobservaties in arena's geven aan dat rood licht loopsnelheid van vrouwtjes significant deed verminderen gelijk aan het effect van wit licht en anders dan nabij-infrarode straling (nir). Loop activiteit en lengte van pauzes werden ook beïnvloed door de stralingsbron, met een significant verschil tussen nir en wit licht, en met tussenliggende

waardes in rood licht. Deze resultaten geven aan dat *P. melanarius* zich verschillend gedraagt onder de drie stralingsbronnen wat suggereert dat nir in plaats van rood licht het meest geschikt is voor het meten van gedrag in totale duisternis.

Hoofdstuk 3 gaat over een merk-terugvang proef met *P. melanarius* in een enkel veld triticale (x *Triticosecale* Wittmack.). Motiliteit werd afgeleid door invers-modelleren van een Fokker-Planck diffusie model. Het resultaat werd vergeleken met motiliteit berekend uit de gekwadrateerde verplaatsingsafstanden en de tijd tussen loslaten en terugvangen. Deze twee methodes, gebaseerd op verschillende principes, resulteerde in vergelijkbare resultaten. Dit versterkt het vertrouwen in motiliteit als een bruikbaar concept voor het kwantificeren van dispersie snelheid van loopkevers. Een meta-analyse van literatuur data werd gebruikt voor het identificeren van belangrijke factoren die loopsnelheid van loopkevers beïnvloedt. De meta-analyse liet zien dat motiliteit van loopkever soorten in akkers drie keer zo groot is als motiliteit in een bebost gebied. De meta-analyse liet geen consistente verschillen zien in motiliteit op het niveau van individuele soorten, en het groeperen van soorten naar geslacht en grootte liet geen significant effect zien van deze factoren.

Hoofdstuk 4 behandelt het verdelingspatroon van *P. melanarius* gemonitord tussen naast elkaar gelegen velden met rammenas (*Raphanus sativus*) en rogge (*Secale cereale*) in een merk-terugvang experiment. Modelselectie werd gebruikt voor het onderscheiden van gedrag op de habitatovergang. Een studie aan loopgedrag in experimentele arena's, door middel van het in hoofdstuk 2 gepresenteerde observatie systeem, complementeert de veldstudie. Dispersie in het veld werd toereikend beschreven door een Fokker-Planck diffusie model met gelijke motiliteit in de beide gewassen en een voorkeur voor rammenas boven rogge op de overgang tussen de twee gewassen. Kevers verplaatsten zich 1.5 keer vaker van rogge naar rammenas dan omgekeerd. Analyse van video tracking data resulteerde in geschatte waardes voor motiliteit die, wanneer opgeschaald, dicht in de buurt lagen van de waardes verkregen uit het veld. Daarnaast wees de arena data op een grotere frequentie van habitat binnenkomst in rammenas in vergelijking met rogge. De studies op de kleine en grote schaal gaven dus kwalitatief en kwantitatief vergelijkbare resultaten.

Hoofdstuk 5 beschrijft de invloed van habitat compositie op dispersiegedrag binnen het groeiseizoen in een merk-terugvang experiment in een agrarisch landschapsmozaïek dat bestond uit meerjarige grasstroken en verschillende gewassoorten met verschillende grondbewerking. Beschikbaarheid van voedsel per habitat werd geschat uit het gewicht van de van nature voorkomende kevers. Modelselectie in een set van diffusiemodellen met

motiliteit, gedrag op de grens en verlies van kevers werd gebruikt voor het identificeren van functioneel verschillende habitat eenheden. Semi-natuurlijke grasranden waren functioneel anders dan gewashabitatten. Motiliteit was lager in de randen dan in de gewashabitatten, en op de gewas-rand overgang liepen meer kevers naar het gewas dan naar de rand wat betekent dat de rand zich gedraagt als een barrière voor verspreiding. In de gewashabitatten verschilde de motiliteit tussen velden, maar er is geen consistente relatie gevonden met gewicht van kever als indicator voor voedsel beschikbaarheid evenals met grondbewerking. Gebaseerd op de motiliteit in de gewashabitatten wordt de verplaatsing van *P. melanarius* gedurende een groeiseizoen in een landschap zonder semi-natuurlijke habitatten geschat op ongeveer 100-160 m. Gegeven deze range is er weinig herverdeling van kevers te verwachten tussen velden binnen een groeiseizoen, vooral als de velden omgeven zijn door grasranden of heggen. Dit betekent dat het succes van biologische bestrijding door deze soort meer afhankelijk is van de invloed van het management van velden op lokale populatiedynamiek dan van habitat heterogeniteit.

Hoofdstuk 6 presenteert een synthese van de voorgaande hoofdstukken en bediscussieert dispersiegedrag van loopkevers in relatie tot landschapsheterogeniteit. Er is speciale aandacht voor het proces van populatie uitwisseling tussen habitatten. Voor de populatie uitwisseling tussen gewashabitatten en semi-natuurlijke grasranden leek de grote van de bias op de overgang gerelateerd te zijn aan de motiliteit in het gewas. De vermenigvuldigingsfactor voor motiliteit op de gewas-rand overgang nam met dezelfde factor toe als motiliteit in de gewashabitatten voor twee van de drie overgangen. Dit betekent dat de permeabiliteit van de grasranden lijkt toe te nemen met toenemende motiliteit in het veld. Op de mosterd-gerst (gewas-gewas) overgang was de voorkeursrichting naar het habitat met de laagste motiliteit, wat suggereert dat ook in dit geval een hoge motiliteit resulteerde in een hoge preferentie om te vertrekken.

In deze studie is dispersie van een grond predator gekwantificeerd op basis van dispersie gedrag binnen en tussen habitatten gedurende de zomer en herfst. Ik heb laten zien dat dispersie over habitatgrenzen wordt bepaald door een verschil in motiliteit tussen habitatten en een voorkeur op een habitatovergang. Toekomstige studies zouden in detail moeten kijken naar de oorzaken van verschillen in motiliteit tussen habitatten en naar factoren die de voorkeur op habitatovergangen beïnvloedt door dispersiegedrag en habitat eigenschappen simultaan te vergelijken in gerepliceerde veldproeven en voor verschillende momenten gedurende het jaar.

Het resultaat van dit onderzoek is een methodologische aanpak om dispersiegedrag van insecten in een heterogene omgeving te kwantificeren op basis van merk-terugvang data en invers-modelleren. De combinatie van modellen en data kan leiden tot de ontwikkeling van voorspellende dynamische modellen voor populatieverspreiding van insectenetende arthropoden. De uiteindelijke stap is om deze modellen voor populatieverspreiding te integreren met tools waarin alternatieve landscapesconfiguraties worden afgewogen tegen meerdere doelstellingen om zodoende een ruimtelijke rangschikking van landgebruik te vinden die de ecosystemedienst van biologische plaagbestrijding maximaliseert binnen een breder kader van landschapsfuncties.

List of publications and presentations

Articles in refereed SCI journals:

Allema A.B., Rossing W.A.H., van der Werf W., Heusinkveld B.G., Bukovinszky T., Steingröver E., van Lenteren J.C. 2012. Effect of light quality on movement of *Pterostichus melanarius* (Coleoptera: Carabidae). *Journal of Applied Entomology* 136, 793-800.

Articles in non-SCI journals:

Oomen G. 2014. Loopkevers moeten op de akker zelf worden gekoesterd, want hun actieradius is beperkt. *Ekoland* 1, 36-37. (based on an interview)

Papers at conferences and symposia, published in full in proceedings:

Berghuijs H.N.C., Allema B., Hemerik L., van der Werf W., Groot J.C.J., Rossing W.A.H. 2012. Fokker-Planck model for movement of the carabid beetle *Pterostichus melanarius* in arable land: model selection and parameterization. *Proceedings Netherlands Entomological Society Meeting* 23, 21-28.

Allema, A. B., Rossing W., van der Werf W., Volker D., Marsan J., Steingröver E., van Lenteren J. 2010. Ground beetle dispersal: how to bridge the scales? *Proceedings of the meeting of the working group Landscape management for functional biodiversity IOBC-WPRS Bulletin* 56, 5-8.

Allema, A. B., Rossing W., van der Werf W., Bukovinszky T., Steingröver E., van Bruggen A., van Lenteren J., Booij K. 2008. Model for integrating internal and external drivers for dispersal and distribution pattern in carabid beetles. *Proceedings of the meeting of the working group Landscape management for functional biodiversity IOBC-WPRS Bulletin* 34, 5-8.

Papers at conferences and symposia, published as abstracts:

Allema, A.B., Rossing W., van der Werf W., Bukovinszky T., van Lenteren J. Influence of red light on night activity of *Pterostichus melanarius* (Coleoptera: Carabidae). 2009. 14th European Carabidologist Meeting.

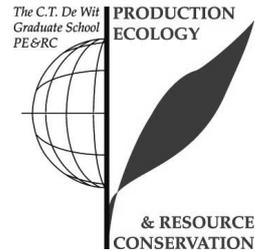
Allema B., Rossing W., Bukovinszky T., van der Werf W., van Lenteren J., van Bruggen A., Steingröver E. 2007. Linking pest suppression to landscape configuration by considering movement behaviour of ground beetles. AAB conference: Theoretical population ecology & practical biocontrol – bridging the gap.

Media

Noorderlicht nieuws. Televisie reportage door verslaggever Remy van den Brand over het loopkeveronderzoek van B. Allema. 02-07-2009, *Nederland* 3, VPRO.

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)



Review of literature (4.2 ECTS)

- Model for integrating internal and external drivers for dispersal and distribution pattern in carabid beetles, presented at the IOBC-WPRS meeting on Landscape Management for Functional Biodiversity in Bordeaux, France (2008)

Post-graduate courses (5.1 ECTS)

- Introduction to R for statistical analysis; PE&RC (2008)
- Spatio-temporal models in ecology; PE&RC (2009)
- Spatial ecology; PE&RC (2011)
- Introduction to Bayesian statistics; PE&RC (2011)

Laboratory training and working visits (2.6)

- Taxonomy Carabidae; PPO, Lelystad (2007)
- Modelling ground beetle walking behaviour; Agricultural University, Uppsala (2008)
- Ethovision software; Noldus, Wageningen (2008)

Invited review of (unpublished) journal manuscript (1 ECTS)

- Insect Conservation and Diversity: biodiversity and species traits in an agricultural environment (2013)

Deficiency, refresh, brush-up courses (3 ECTS)

- Advanced population dynamics (2008)
- System analysis, simulation and system management (2009)

Competence strengthening / skills courses (2.6 ECTS)

- Writing a research proposal; WGS (2008)
- PhD Competence assessment; WGS (2008)
- Scientific writing; WGS (2011)

PE&RC Annual meetings, seminars and the PE&RC weekend (3 ECTS)

- PE&RC Days (2007-2009 and 2011)
- PE&RC Weekends (2008-2012)

Discussion groups / local seminars / other scientific meetings (7.5 ECTS)

- Ecology discussion group; Forest and Nature conservation (2008-2011)
- Insect-Plant interactions (2007-2011)
- Spatial Methods (SPAM) (2008-2011)
- Animal Movement Ecology (2011-2012)
- Quantitative Analysis of movement (QAM) (2009-2010)
- Nederlandse Entomologendag (2007-2011)

International symposia, workshops and conferences (4.2 ECTS)

- Theoretical population ecology & practical biocontrol – bridging the gap; poster presentation; Warwickshire (2007)
- IOBC Landscape management for functional biodiversity; oral presentation; Bordeaux (2008)
- European carabidologist meeting; poster presentation; Westerbork (2009)
- IOBC Landscape management for functional biodiversity; oral presentation; Cambridge (2010)

Lecturing / supervision of practical's / tutorials (3 ECTS)

- System analysis, simulation and systems management; lecturing and computer practicals (2009-2012)

Supervision of MSc students

- Modelling the dispersal of carabid beetles in a heterogeneous landscape mosaic, using partial differential equations (2011)
- Analysing walking behaviour of *Pterostichus melanarius* (2011)

Photo illustrations

- a. *Pterostichus melanarius* marked with a retro-reflector.
- b. *Pterostichus melanarius* marked with nail polish.
- c. Field experiment in triticale under sown with grass/clover, with in the front a trapping cross.
- d. Interface between the adjacent fields of rye and oilseed radish with two pitfall traps.
- e. Arenas planted with rye in the front and oilseed radish in the back.
- f. Grass field margin with hedgerow in the habitat mosaic field experiment.
- g. Grass field margin without hedgerow in the habitat mosaic field experiment.
- h. Interface between barley and yellow mustard in the habitat mosaic field experiment.



Funding and colophon:

This project was financially supported by strategic research funds of the C.T. de Wit Graduate School for Production Ecology and Resource Conservation, and co-financed by the DLO Research Programme for LNV, subtheme: Sustainable development and adaptation of ecosystems and landscapes in a metropolitan context (KB-01-008-024-ALT).

Cover design: Erika van Gennip

The ground beetle on the cover is adapted from a picture of *Pterostichus melanarius*
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