



Incorporating behaviour into simple models of dispersal using the biological control agent *Dicyphus hesperus*

Brian O. Ma^{a,*}, Brad H. Davis^{b,e,1}, David R. Gillespie^c, Sherah L. VanLaerhoven^d

^a Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada

^b Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

^c Pacific Agri-Food Research Centre, Agriculture and Agri-Food Canada, Agassiz, BC V0M 1A0, Canada

^d Biological Sciences, University of Windsor, Windsor, ON N9B 3P4, Canada

^e Biotechnology Institute, University of Minnesota, Saint Paul, MN 55108, USA

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ABSTRACT

We explored the utility of incorporating easily measured, biologically realistic movement rules into simple models of dispersal. We depart from traditional random walk models by designing an individual-based simulation model where we decompose animal movement into three separate processes: emigration, between-patch movement, and immigration behaviour. These processes were quantified using experiments on the omnivorous insect *Dicyphus hesperus* moving through a tomato greenhouse. We compare the predictions of the individual-based model, along with a series of biased random walk models, against an independent experimental release of *D. hesperus*. We find that in this system, the short-term dispersal of these insects is described well by our individual-based model, but can also be described by a 2D grid-based biased random walk model when mortality is accounted for.

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1. Introduction

Behavioural ecologists have long understood that dispersal is often an environment-dependent strategy undertaken to increase fitness. Dispersal dynamics have major implications in ecology, from the management of pests, conserved species, and species invasions (Skalski and Gilliam, 2003) to disease epidemiology (Ostfeld et al., 2005). Much attention has been given to understanding the complex interactions between landscape structure and animal behaviour (Kareiva and Wennergren, 1995; Lima and Zollner, 1996; Vuilleumier and Metzger, 2006). This has resulted in a variety of modelling approaches including random walks (Mills et al., 2006; Codling et al., 2008).

Random walk (RW) models begin with simple rules governing animal movement and dispersal, and are based on the assumption that movement is random and the habitat is relatively homogeneous (Kareiva, 1983; Mills et al., 2006; Codling et al., 2008). However, there has been extensive work on incorporating more complex habitat structure (e.g., Turchin, 1991; Skalski and Gilliam, 2003; Vuilleumier and Metzger, 2006; Barraquand and Benhamou,

2008; Ovaskainen, 2008) and individual behaviour (e.g., Kareiva and Shigesada, 1983; Lima and Zollner, 1996; Zollner and Lima, 1999; Byers, 2001; Codling and Hill, 2005) into models of dispersal (reviewed by Codling et al., 2008). For instance, correlated random walk (CRW) models are based on the idea that an individual's previous movement direction influences the direction of its next movement (Codling et al., 2008), which can be due to the tendency of animals to move forward (Bovet and Benhamou, 1988). Correlated random walks often result in greater dispersal than uncorrelated random walks, although the degree of correlation decreases as patch density increases (Zollner and Lima, 1999). Kareiva and Shigesada (1983) used a CRW model to describe *Pieris rapae* (cabbage white butterfly) movement. Biased random walks are also used to model dispersal, and these models are based on the idea that the probability of movement in a particular direction is more likely (Codling and Hill, 2005; Benhamou, 2006; Codling et al., 2008). This directional preference can be based on fixed environmental factors (Codling et al., 2008), a gradient of chemotaxis (Macnab and Koshland, 1972), or individual choice in direction at each step (Turchin, 1991; Benhamou, 2003, 2006).

One perceived shortcoming of RW models is that movement behaviour is oversimplified, where movement is often reduced to a single parameter (Bowler and Benton, 2005) and does not account for decision-making processes of individuals. Furthermore,

* Corresponding author. Tel.: +1 778 772 4512; fax: +1 778 782 3496.

E-mail address: bom@sfu.ca (B.O. Ma).

¹ These authors contributed equally, but in different capacities, to this manuscript.

the behaviour of an individual is thought to be more important than the spatial structure of the habitat when scaling up movement patterns (Morales and Ellner, 2002). Organisms are typically able to assess their current and immediate surrounding environments and then make a decision on when and where to disperse, and on a fundamental level, dispersal behaviour can be subdivided into three related but independent stages: (1) the decision to emigrate, (2) between-patch movement (taxis) and (3) the decision to immigrate (Bowler and Benton, 2005; Schick et al., 2008). The conditions that affect each of the three stages are not likely to be wholly independent of one another, but nonetheless, each is a separate process to some degree. It is not clear if the outcomes of dispersal decisions are sensitive to the behaviour at each stage or if overall dispersal behaviour is sufficiently robust that the outcomes can be described by models that reduce these behaviours to a single function; therefore, the objective of this study is to determine whether incorporating the biological details of dispersal can provide us further insight into animal dispersal.

We develop a protocol for measuring emigration, between-patch movement, and immigration, and then incorporate the functions describing each of these processes into an individual-based model simulation. We design, parameterize, and test our individual-based model of dispersal using a single species, which to our knowledge has not been done before (Bowler and Benton, 2005). We use the experimental data of a biological control agent, *Dicyphus hesperus* Knight (Hemiptera: Miridae) in a 2D grid structured tomato greenhouse environment to determine patch movement rules, and we test our model against a biased random walk model and experimental data from an independent greenhouse release experiment to determine the predictive power of our model.

Our study system is suitable for studying dispersal because *D. hesperus* will readily disperse in a greenhouse although most of the dispersal rules used by these insects are unknown. *D. hesperus* is an omnivorous true bug that preys on a variety of small arthropods and has been shown to be a good biological control agent of *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae) in glass greenhouses (McGregor et al., 1999; Sanchez et al., 2003). *D. hesperus* are able to prey on whitefly populations situated on these plants and will also feed on plant tissue; however, they are unable to complete their life cycle in the absence of prey (Gillespie and McGregor, 2000; Sanchez et al., 2004). Under those circumstances, it is necessary for them to disperse to find resources necessary for survival and reproduction. The crop plants in our study system are tomato and mullein: tomato plants are of commercial importance to greenhouse growers, and mullein, *Verbascum thapsus* L. (Scrophulariaceae), enhances establishment and survival of *D. hesperus* in tomato crops (Sanchez et al., 2003). Crop plants are typically arranged in rows of plants set side-by-side with every second row separated by walking space; thus, the spatial structure can be described as a simple matrix with each plant (i.e., patch) corresponding to a cell.

2. Methods

The methods are presented in two parts. First, we present the model, adhering to a formalized protocol for presenting individual-based models as closely as possible (Grimm et al., 2006). In this section, we also present the experiments used for parameter estimation that is used in the model we present. Second, we present the methods to compare the model against other models (based on a biased random walk), and describe the experimental protocol used for a greenhouse release of *D. hesperus* which the models are compared against.

2.1. The model

2.1.1. Purpose

To develop a spatially explicit individual-based computer simulation (SE-IBM) to model *D. hesperus* dispersal dynamics within a greenhouse. We refer to this model as the EBI model to reflect the three steps involved in movement between patches in this model: (1) the decision to emigrate from the current patch, (2) between-patch movement (i.e., taxis) towards their newly selected patch, and then (3) immigration onto the new patch. This model can be used to make predictions about the expected percentage of pest-species host plants that are presently occupied or have ever been occupied by the focal species through time. We compare the predictions of the SE-IBM model to a biased random walk model and experimental releases of *D. hesperus* in small and large greenhouse environments.

2.1.2. State variables and scales

Space is modelled as a matrix with R rows and C columns with reflecting boundaries such as exist in a real greenhouse. Fig. 1 illustrates the topographical map of both a small and large greenhouse layout. Each of the $R \times C$ patches (which correspond to either a single plant, or a section of empty walkway that is the same size as a plant) that comprise the landscape are defined by (1) the attractiveness of the cell ($\gamma_{r,c}$), and (2) the probability of exiting the occupied patch during the first time step spent on the patch (α_k), and the decay-rate constant used to describe how the probability of exiting the patch changes through time (β_k). We assumed that there was no density or frequency-dependence between individuals, and therefore each individual was modelled separately. Individuals are described by three variables: their current row coordinate (r_i), their current column coordinate (c_i), and the amount of time they have spent on their currently occupied patch, t_{patch} .

2.1.3. Processes

The simulation model proceeds by stepping through hourly time steps. Within each time step, the simulation model evaluates each individual's survival, determines if they will emigrate from their currently occupied patch, and if they do exit their current patch then evaluation of the surrounding patches (i.e., taxis), and immigrate into a new patch for every surviving member of the population (Fig. 2). We assume that if movement occurs, it is in a fixed step length of one patch per unit time.

2.1.4. Initialization and model details

We used the parameter estimates and functions described in the previous section to parameterize the model. The model was initialized and sampled to reflect the experimental protocol of the small and large greenhouse experiments. In the greenhouse experiments, mullein plants were positioned in the center of four tomato plants, and as such did not conform to a particular $R \times C$ coordinate. To accommodate this, we used a weighted composite for the attraction score and the parameters determining the exit probability of one mullein plant and its four surrounding tomato plants of 80% of the tomato's value and 20% of the mullein plant's value. This is because each cell now contains 1 full tomato plant and 0.25 mullein plants (e.g., $1/1.25 = 0.8$).

The number of plants visited by *D. hesperus* was counted every 72 h, and only for the cells that were sampled in the experiment. We used open boundaries where *D. hesperus* were allowed to leave the region of counted cells. For each patch, we recorded whether it is, currently or has previously, been visited. Small greenhouse simulations were replicated 8 times. Large greenhouse simulations were replicated 11 times.

Within a given patch, individuals that survived were given the opportunity to move based on the decision-making process derived

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