

Movement and egg laying in Monarchs: To move or not to move, that is the equation

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Abstract Monarch butterfly (*Danaus plexippus*) populations are in decline in agricultural landscapes, in which genetically modified crops that are resistant to herbicides ('Roundup Ready') have resulted in the decimation of milkweed (*Asclepias* spp.) hosts over large areas due to the increased use of glyphosate. Movement is the key ecological process linking individual fitness traits to the utilization of sparse resources distributed across landscapes with emergent population level consequences. Often, movement ecology is highly simplified or even abstracted into a simple rate of flow between populations (i.e. a metapopulation) separated by a hostile 'matrix'. Whereas, we can gain important insights into the population dynamic as a whole if we explore movement as an explicit, complex, behavioural process in which the matrix is not simply a void. We developed a spatially explicit individual-based model to describe host-seeking behaviour over the lifetime of a monarch butterfly, which utilizes hosts both aggregated in patches and scattered across the wider landscape as a substrate for laying eggs. We examine the simulated movement distances and spatial population distribution (eggs laid) as a result of different movement rules (directionality), perceptive distance (ability to find) and landscape configuration (how milkweed is distributed). This indicates the potential consequences of cleaning up the matrix (i.e. the obliteration of non-crop vegetation with Roundup) and changing habitat configurations at a landscape scale on individual movement behaviours and the emergent number of eggs laid, essentially the birth term in any population model. Our model generates movement distances of the order of 12 km commensurate with summer breeding monarchs and suggests that milkweed removal has reduced egg laying by up to 30%. We suggest possible amelioration strategies.

Key words: emergent process, host-finding behaviour, individual-based simulation model, monarch butterfly, movement, spatial ecology.

INTRODUCTION

Increasingly, habitats are being cleared and fragmented by anthropogenic activities. These activities, usually associated with agriculture, urbanization, mining and so forth, directly and indirectly lead to the decline and local extinction of the less vagile species that have specialized habitat requirements (Walter & Zalucki 1999; Sands & New 2002). Approaches to research, conservation and management of such fragmented populations treat the ensemble of the remaining habitat patches as a 'metapopulation', with the persistence of any species depending on a mixture of population dynamics within remnant habitat patches and dynamics across patches, all else being equal (e.g. Hanski 1989, 1999; Hanski *et al.* 1995; Hill *et al.* 1996). However, we consider that metapopulation concepts, which generally ignore the possibility that the area between suitable patches may be less than hostile, are limited in their ability to suggest viable options for habitat restoration beyond patch-focused

recommendations and very general statements about the landscape (see also Shreeve *et al.* 2004). In addition, Hawkes (2009) points out that movement behaviours are more complex than random walk approaches when response to habitat is incorporated and recommends the use of mechanistic, rather than phenomenological, models in the description of dispersal.

In a metapopulation, a species persistence will depend on the size and spatial arrangement of the remaining habitat areas, their rates of creation and destruction, and movement amongst such habitats. The movement process is central to persistence and can be broken down into the likelihood of leaving, traversing a potentially treacherous landscape, often termed the 'matrix' (Driscoll *et al.* 2013), finding new areas (the search process) and utilizing them (Zalucki & Lammers 2010). Metapopulation models do not explicitly treat the background matrix that embeds the usable habitat patches as having any suitable resources, and thus the matrix has no influence on the overall landscape ecology of the species (Wiens *et al.* 1997; Turner *et al.* 2001; Zalucki & Lammers 2010). Some exceptions exist, for example, where the matrix in a metapopulation model has an implicit influence

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Accepted for publication May 2015.

on colonization or dispersal success as a function of distance (e.g. Drielsma & Ferrier 2009) and 'texture' (e.g. Westerberg & Wennergren 2003).

Butterflies have been used as model systems when exploring the interaction of landscape structure and population persistence. Their habitat requirements are relatively well known (Dover *et al.* 1997; Walter & Zalucki 1999; Dennis *et al.* 2003; Shreeve *et al.* 2001). The assumption that butterflies do not use the space between habitats has been questioned (Dennis 2004), although how it is exploited will depend on the biology of the particular species (Dennis *et al.* 2004). As has been pointed out by Dennis (2004), the matrix is not a void and may variously provide suitable nectar and other resources, such as larval host plants that may be utilized.

Here we use a spatially explicit movement model of individual monarchs to investigate the effect of both the amount and the spatial arrangement of resources (patches of habitat) within a landscape on egg laying. The individual-based model of butterfly movement, habitat selection preference and oviposition behaviour was designed to allow us to explore mechanistically the impact of individual movement behaviours on emergent egg distribution in a landscape (see also Stolk *et al.* 2007). Our objective was to consider what happens to persistence of a species if the matrix is cleaned up and made a void, due to say herbicide usage on host plants (e.g. milkweeds) growing in agricultural fields. With Roundup Ready soybeans and corn being widely grown in the north-eastern USA, such extirpation of low-density milkweeds and large patches has occurred (Pleasants & Oberhauser 2012). We created a landscape in which remnant patches of milkweed habitat may still be present in old fields, and along roadside verges, but the area in between has been made clean, a situation analogous to a classic metapopulation. We used a simulation modelling approach to explore some of the theoretical consequences of such clearing and different spatial arrangements of habitat as well as a restoration possibility. Although we had monarchs and milkweeds in mind, we believe there are general inferences that can be drawn for spatially distributed insect populations, their conservation and management.

METHODS

Searching, habitat and landscapes: putting the individual and mechanism back

Background The study system on which we based our model is monarch butterflies, *Danaus plexippus*, in their summer breeding season. The monarch is a highly vagile species that moves extensively amongst patches of host plants, milkweeds (almost exclusively species of *Asclepias*).

Local adult monarch density appears to be aggregated around such patches (Zalucki & Suzuki 1987), as in Root's resource concentration hypothesis (Root 1972). However, monarchs will also leave such areas; patch edges are effectively permeable (Zalucki & Kitching 1982a; Ries & Debinski 2001). The population that resides outside such habitat patches is substantial (Bull *et al.* 1985). Females are likely to have an average birth to death distance of about 11 km (Zalucki 1983), based on mark-recapture studies (Zalucki & Kitching 1985) and models of adult movement over the lifetime of a female in a landscape with a realistic encounter rate of milkweed. Away from milkweed patch habitat, host plants can be found at various low densities: the matrix is not empty (Zalucki *et al.* 1981). These scattered 'single isolated plants' are utilized by monarchs as they traverse the landscape (Zalucki & Kitching 1982b). Such plants can be found along roads and scattered amongst crops and other disturbed areas. Egg numbers per plant in these cases are often high and returns on eggs in terms of survival to the adult stage are better on single plants than for patch plants (Zalucki 1981; Zalucki & Kitching 1982a,b,c; Zalucki & Rochester 2004).

The individual-based model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm *et al.* 2006, 2010). The model was written in Java using the Repast Symphony 2.2 toolkit for agent-based modelling (North *et al.* 2013).

Model purpose The simulation model was developed to simulate the response of an individual (female) monarch 'agent' to habitat availability and configuration in a landscape (both in terms of movement and egg laying decisions), which drives subsequent egg distributions. Based on what we know about monarch movement ecology and behaviours, it was designed to help us predict how the species responds to varying quantities and spatial configuration of sparse habitat in the 'matrix' that is often perceived as a void, and what the emergent consequences are at the landscape for monarch population density and distribution.

Entities, state variables and scales The model consists of monarch agents within a spatial landscape which also comprises landscape patch agents. The model landscape consists of two types of 'patch': 'habitat' and 'matrix' (non-habitat). Suitable habitat patches for monarchs are defined as areas of dense milkweed (growing in patches of various sizes) and the immediate surrounding area of higher density milkweed (Zalucki 1983, 1993). Milkweed patches provide all the species requirements: host food plants available at high density for egg laying, nectar resources for adult feeding, basking sites and mating sites; *sensu* a union of required resource in the one place (Dennis *et al.* 2003). Such milkweed habitat is often found in old fields as part of succession (Bull *et al.* 1985; Suzuki & Zalucki 1986). The matrix (i.e. the remaining area that is not habitat patches) may be empty or contains a low density of milkweed randomly distributed.

We were interested in the extreme effects of habitat availability on the monarch agents. We therefore created landscapes with a low percentage of habitat cover (1%) or high cover (50%). Artificial landscapes were generated following the method of Saura and Martínez-Millán (2000) and were

converted from ascii grids with a cell size of 56 m in a unit universe measuring 11.2 km² to polygon shape files using ArcGIS. Extremes of habitat cover and fragmentation were used in the simulations to explore the effect of landscape configuration on the movement and oviposition behaviours of agents (Table 1). Habitats were either clustered or fragmented for the 50% cover. For the 1% cover landscapes, habitats were also either clustered or fragmented, but we added the extreme of a uniform distribution (Table 1). For each of these landscape types, we ran simulations with the matrix either void or with low density milkweed. The model runs on the artificial polygon landscapes (Fig. 1) and can be easily transferred to other landscapes including digitized real landscapes, simply by altering the spatial input data.

The model ran on a daily time step, with a number of sub-steps relating to movement (see below). The model landscape is a 'torus' – that is, should an individual leave the edge of the square landscape, it is calculated to reappear and continue its movement on the opposite side.

Model parameters (Table 2) define the movement, biology and habitat use of the monarch and landscape patch agents. As several components were not known, we varied these between small and large values to explore their effect on our simulations. Individual monarch agents have the state variables 'daily eggs laid' as well as 'daily distance moved', both of which accumulate each day with the processes of oviposition and movement, to a maximum (Table 2). Individuals were able to query their environment, where individual habitat patches were modelled as 'landscape' agents – the monarch agent would know the host plant preference value of the patch (landscape agent) that it was currently located within by implementing the 'WithinQuery' Repast method, which used the GIS capabilities of Repast to query in which landscape agent the monarch agent was located. The agent was able to query which landscape agents were nearby, using the 'GeographyWithin' method with a specified perception radius, again using the GIS capabilities of Repast to query landscape agents within the perception range buffer;

Table 1. Spatial statistics for the landscapes derived using Patch Analyst 5.1 for ArcGIS 10 (Rempel *et al.* 2012)

	1% cover, uniform	1% cover, 0.35 frag	1% cover, 0.55 frag	50% cover, 0.35 frag	50% cover, 0.55 frag
Cover %	1	1	1	50	50
Fragmentation	uniform	0.35 (less clustered)	0.55 (more clustered)	0.35 (less clustered)	0.55 (more clustered)
Number of patches: habitat	397	48	20	220	168
Number of patches: matrix	1	1	1	195	143

This is the order (from left to right) in which landscapes appear in the Results section.

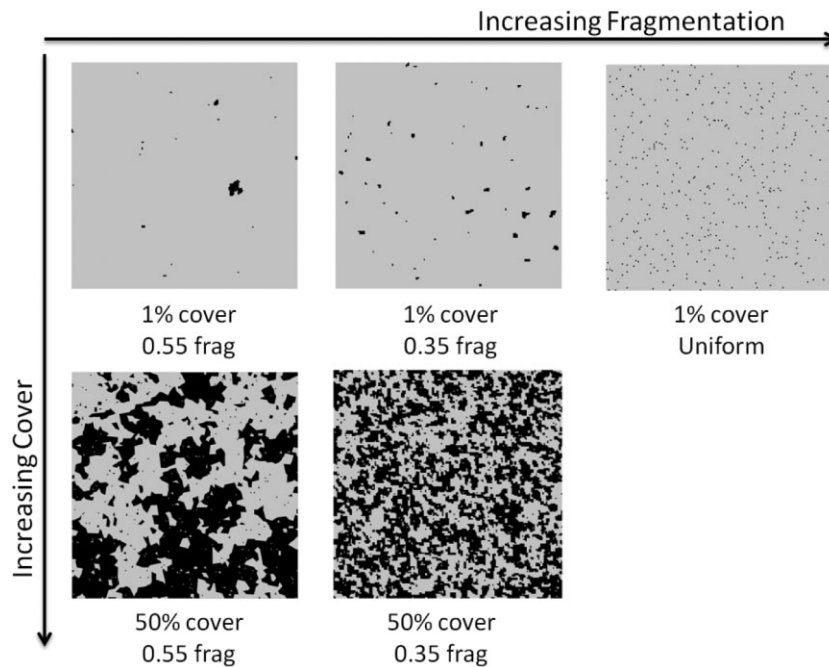


Fig. 1. Artificial landscapes used in the simulations (see Table 1 for descriptions and details). The dark areas are suitable habitat patches, the grey is matrix. Landscapes vary in fragmentation or degree of clustering and percentage cover from low (1%) to high (50%).

Table 2. Overview of model parameters that define movement of a monarch agent

Parameter	Values	Source
Movement parameters		
Perception distance	5 m (short) and 25 m (long)	Zalucki & Kitching (1982b)
Field of view	$\pm 30^\circ$ (narrow) and $\pm 120^\circ$ (wide)	n/a
Directionality	0.2 (low) and 0.8 (high)	Zalucki and Kitching (1982b)
Step length	50 m (short) and 125 m (long)	n/a
Daily distance max	15 000 m	Based on the estimated limit of a mark-recapture study for monarchs (Zalucki & Kitching 1985)
Monarch agent parameters		
Eggs laid per day (max)	100	Based on a 14-day lifespan with a total of 1400 eggs (Zalucki 1981)
Lifespan	14 days	Zalucki (1981); Zalucki <i>et al.</i> (1986)
Total eggs (max)	1400	Zalucki (1981); Zalucki <i>et al.</i> (1986)
Egg laying rate	1 egg per 2.5 m	Zalucki & Kitching 1982a,b)
Landscape parameters		
Percentage habitat cover	1% and 50%	Selected to represent extreme values of lots of habitat (50% of the landscape) and much reduced (1% of the landscape)
Percentage habitat fragmentation	0.35 (fragmented), 0.55 (clustered) and 0 (uniform)	Different spatial arrangements from clustered to uniform
Landscape agent parameters		
Preference value: habitat	1.0, 0.5 and 0.1	Arbitrary (see text)
Preference value: matrix	0.01 and 0	Zero represents a clean matrix and 0.01 is a matrix with randomly distributed single plants

Default values and source given.

for more details on these methods, see the Repast documentation available online and the classes in the repast.simphony.query.space.gis package.

Process overview and scheduling The flow diagrams (Fig. 2) detail the model processes and how they were scheduled. Model parameters defined the movement, biology and habitat use of the monarch agent. These were based on monarch butterflies (Table 2), but as many components were not known, we varied these between small and large values to explore the effect on our simulations.

In the Egg-Laying sub-model (Fig. 2), the eggs laid per step (*eggsPerStep*) were a function of an estimated egg density (1 per 25 plants), where 25 plants were assumed to occupy 2.5 m (thus *egg Density* = 1 per 2.5 m). This was scaled to the *stepSize* (in m) of the movement sub-model:

$$\text{eggsPerStep} = \text{stepSize} \times \text{eggDensity}. \quad (1)$$

Eggs were laid at this fixed rate per movement step; however, a probability based directly on the preference value of the current patch (landscape agent) that the monarch agent was within (see Table 2) determined whether the agent laid eggs during any given step.

The algorithm for movement was based on multiple movement steps within the 'daily' time step of the model. The movement steps end when the daily egg deposition limit was reached (i.e. 100) or the limit to the movement distance per time step was exceeded (i.e. 15 km; see Table 2). The maximum movement distance was increasingly limited in a linear fashion each day, as the agent aged. This was an arbitrary estimate, based only on our limited knowledge of lepidopteran capacity for flight, which is known to decline over

time (e.g. Sappington & Burks 2014). The equation for the estimated decline in maximum daily distance moved is

$$\text{Dist}_{\max} = -1076.9t + 16077, \quad (2)$$

where t is the number of time steps (days) since the simulation began and the lower limit for the maximum daily distance moved is estimated as 1 km.

The preference of the current patch, relative to adjacent patches (but limited to within a perception range), influenced whether a monarch would stay within or leave the current location, and ultimately egg density (Fig. 3). The decision to stay or leave the current patch was based on the equation:

$$P(\text{leave}) = \frac{\text{Pref}_B}{\text{Pref}_B + \text{Pref}_A}, \quad (3)$$

where $P(\text{leave})$ is the probability that the agent will leave the current patch, Pref_B is the preference value for the alternate patch (within perceptive distance) and Pref_A is the preference value for the current patch, where small values of Pref_B are moderated in the model to allow a minimal probability of leaving even when preference is very low, so that $0.1 \leq \text{Pref}_B \leq 1$. If the agent chose to move towards the alternate patch, it searched within the restrictions of the perception angle to locate a direction that would take it towards the alternate patch (Fig. 3a). The agent would then move the step distance in the selected direction. If it did not choose to move towards the alternate patch and so 'returned' to the current patch, it would search with a full 180 degree perception angle, and once it located a direction that would take it towards the current patch, it would move towards it with the step distance in that direction. In either case, if after 100 tries the selected patch was not located, then the agent would 'give up' and continue with a correlated random walk, which could happen

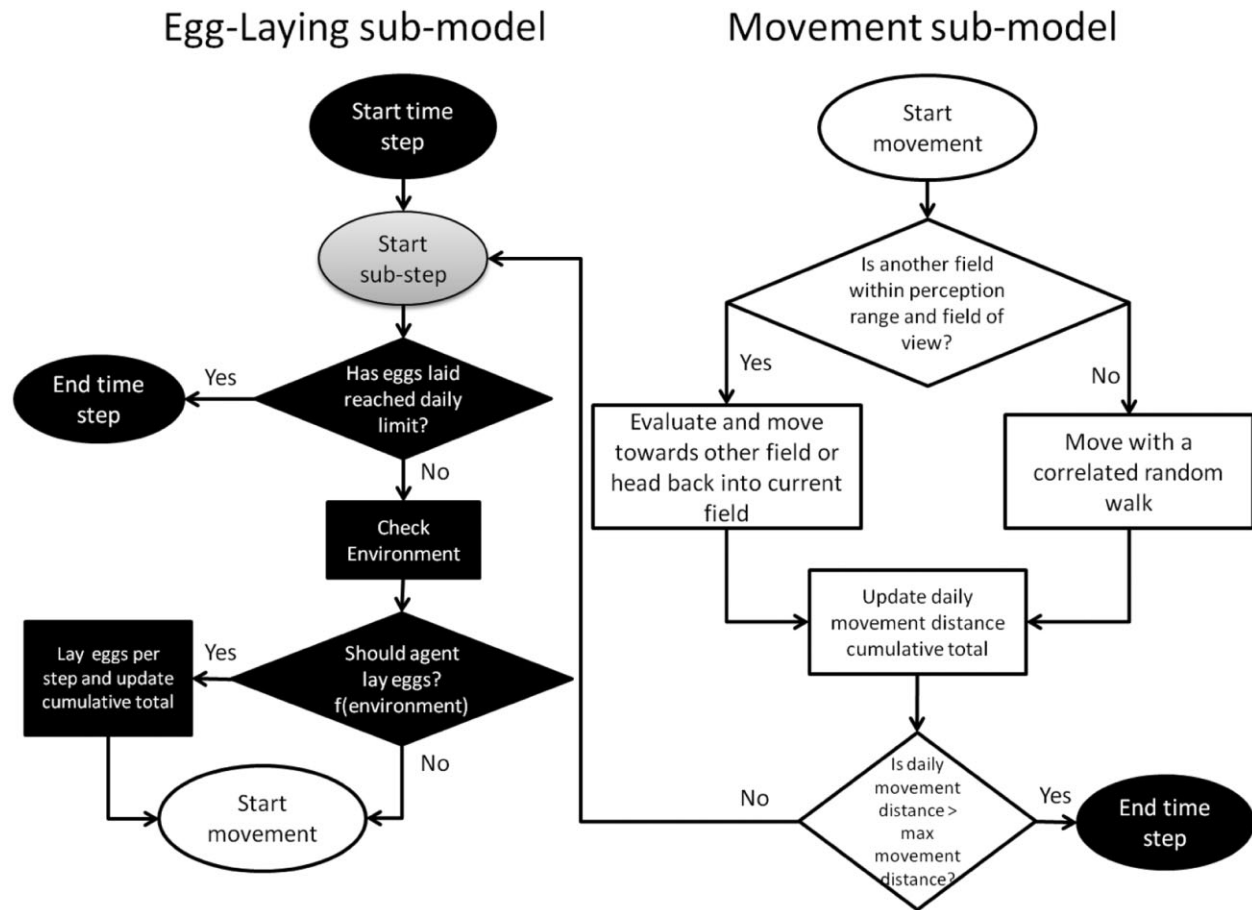


Fig. 2. Flow diagram of model process (egg laying and movement) and scheduling that define the movement of a monarch agent over each daily time step from birth to death.

if there was only a very small amount of the target patch within the movement range.

The correlated random walk was calculated by modifying the current heading by a change in direction, θ . This was calculated in radians as follows and then converted to degrees, with a 0.5 probability of being positive or negative (symbolized by \pm):

$$\theta = \pm\pi R(1 - D), \quad (4)$$

where directionality D is a variable (Table 2) and R is a uniform random number between 0 and 1 (after Zalucki 1983).

Design concepts The model was designed to explore the influence of habitat type and configuration on the movement behaviours of monarchs. The model simulated:

- Habitat selection
- Dispersal and movement
- Oviposition behaviours

Basic principles The model relates to ideas of optimal foraging theory, although in this model there was no resource

depletion. We simulated how an individual decides whether to stay at its current location or move on to another, in this case driven by its need to oviposit/forage in relation to its localized knowledge of the current and surrounding habitat patch quality.

Emergence The primary results of the model, dispersal distances and egg distribution/density, emerged from the simulated movement ecology and behaviour of the individual monarch agents in relation to the habitat characteristics and spatial configuration of the landscape agents.

Adaptation Monarch agents adapt to the landscape in terms of movement pathway and change in direction.

Objectives The movement and foraging behaviours were implicitly fitness-seeking, that is, assuming that the individual had an objective to maximize egg laying/foraging within the shortest amount of time in optimal habitat.

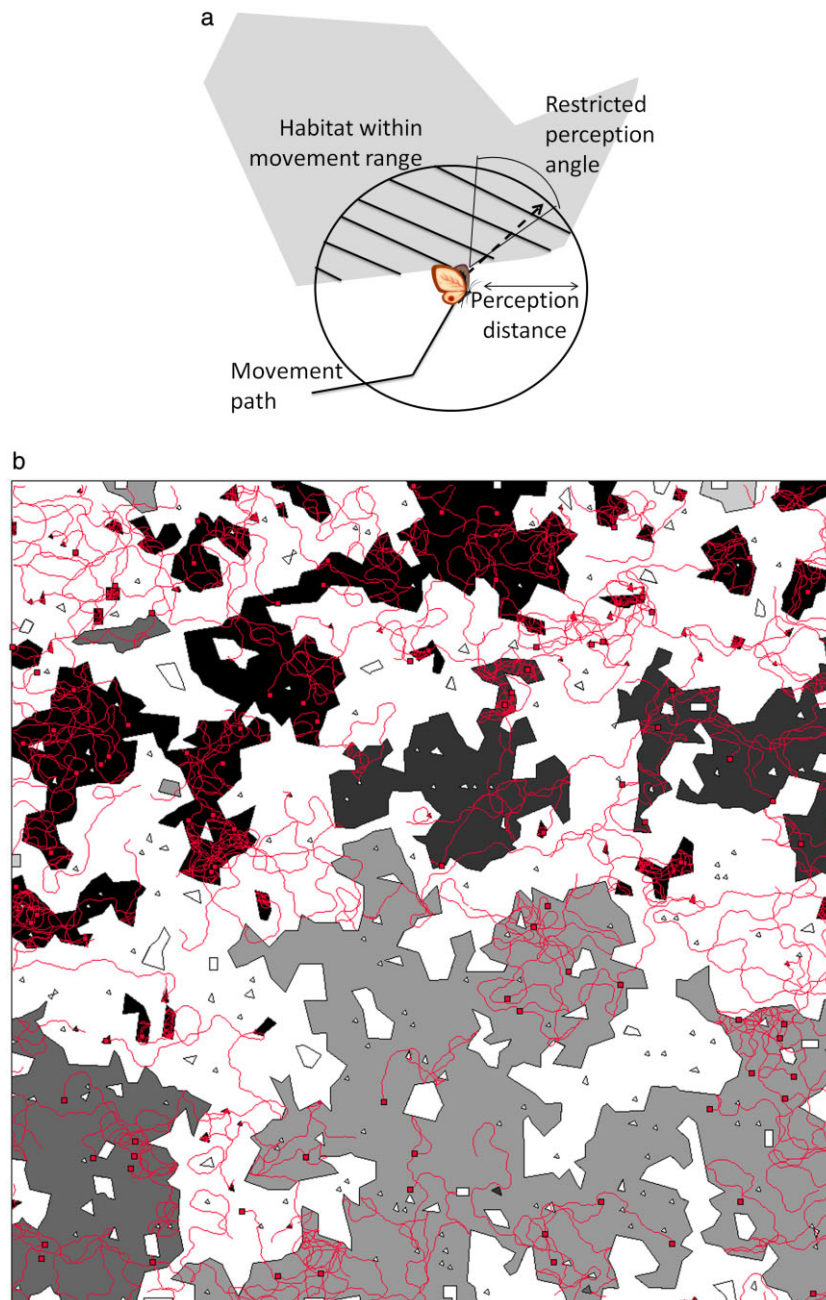


Fig. 3. (a) Illustration of the movement search behaviour in movement sub-model (Fig. 2). The monarch agent has a perception distance (Table 2) but the region that can be searched is restricted according to a perception angle. The agent decides whether to stay or leave the current patch (e.g. matrix) based on Eqn 3, and in the case that it leaves, it will head towards the alternate patch (e.g. habitat) with its path restricted to the perception angle. (b) Model graphical output showing habitats, monarch agents (little red squares) and movement pathways (in red) as well as egg density on a greyscale, the darker the colour, the higher the density.

Learning/prediction This was not represented in the foraging model (e.g. memory of favourable habitat patches): this could be added in future versions of the model.

Sensing Monarchs were able to query the properties of the patches in the landscape within a radius of their current location (their perception distance), within which they were

assumed to have perfect knowledge of the patches/matrix location and properties.

Interaction Agent interaction occurred when monarch agents queried landscape agents to determine the patch properties, which informed the movement rules and oviposition probability. Landscape agents also summed the

number of monarch agents and the total eggs laid within their bounds each day, for output purposes.

Stochasticity The generation of the artificial landscapes was partly stochastic in terms of the placement of the patches and their size. The movement pathway and step size was primarily a correlated random walk, which was stochastic, that takes into account behavioural response to landscape. This response to landscape also had a stochastic element, where a change in direction at a boundary was probabilistic. The number of eggs laid each step was also probabilistic based on the properties of the current patch.

Collectives There were no collectives in the model.

Observation Graphical output of the model showed the landscapes with habitat patches and matrix visualized in different colours (greyscale in Fig. 3b). For each individual, movement pathways were captured in the spatial model output as lines, to visualize the movement pathway results of the sub-daily steps (Fig. 3b). The total daily movement distance was recorded; both direct movement distance from the initial start location to the final location, allowing for wrapping around the torus, and total movement distance over all daily steps. Egg densities were captured in the spatial output as well as a record of the total number of eggs laid in each habitat type (matrix or patch) for each step of the simulation (for each individual).

Initialization The initial population in the model could be varied from one to tens of thousands of agents. The model was initialized using the batch run capabilities of the Repast toolkit to simulate over the entire parameter space, with a fixed number of monarch agents (100) added to the land-

scape at random locations for each of the five landscapes for each iteration. Each iteration of the model was run for a fixed period of 14 days (the typical lifespan of a monarch).

We used the model to address three questions:

Q1: How do the matrix properties and landscape structure influence the simulated movement behaviour of monarchs? We analysed the output of (lifetime) movement distance in relation to the range of simulated monarch behaviours (habitat preference, perception distance, step length and directionality) and landscape properties (% habitat, fragmentation, quality of matrix).

Q2: What are the implications of this movement response to matrix properties and landscape structure for the distribution and total number of eggs laid?

We analysed the output of total eggs in relation to the range of simulated monarch behaviours (habitat preference, perception distance, step length and directionality) and landscape properties (% habitat, fragmentation, quality of matrix).

Q3: What are the implications for conservation of monarchs? We use the simulation model to evaluate a possible conservation measure.

We compared results of the model both with and without a management scenario and quantify the benefit in terms of increased eggs laid (realized fecundity).

RESULTS

Q1 The question of scale: how far does a monarch (agent) fly?

Of the factors tested with the simulation model, directionality and percentage habitat covered appear to be critical to how far a monarch flies (Fig. 4). A

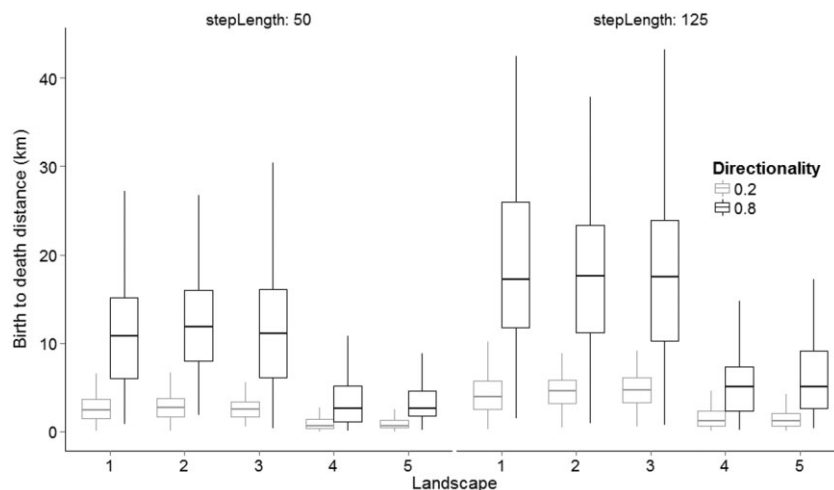


Fig. 4. Box and whiskers plot of straight-line distance (km) from birth (location where an agent starts) to death (location after 14 days) in 5 landscape types: 1 = 1% cover, uniform; 2 = 1%, fragmented; 3 = 1%, clustered; 4 = 50%, fragmented; 5 = 50%, clustered (see Table 1 for details). The simulations depicted for each landscape type by directionality (0.2) and (0.8) for each step length (50 m, right hand panel, 125 m left hand panel). Each bar is an average over 100 (replicate) agents for each of 3 preference levels, 2 perception distance and 2 perception angles (700 agents total).

clean matrix had a marginal effect on distance moved compared to a matrix with a low level of remnant plants; a clean matrix only adds, on average, 240 m to the birth to death distance travelled (range 0–1 km) when compared to equivalent landscapes and movement parameters in the model (results not shown); as the quality of the matrix did not appear to influence movement distance greatly, we present the finding for the clean matrix landscapes only (Fig. 4).

In the simulations, mean straight-line ‘birth to death’ distance increased with age, but the model constraint on distance flown with age (Eqn 2) means that by 8 days (just over half their lifetime), agents have achieved 85% of their total distance (results not shown). We present the total birth to death distances over 14 days below.

A few things stand out from the simulation results: (i) Lifetime ‘birth to death’ distances (from where an agent first starts to its position after 14 days) were short (on average 1–6 km) for landscapes with high (50%) habitat cover (landscapes 4 and 5 in Fig. 4) and much longer (3–18 km) for those with low (1%) cover (landscapes 1, 2 and 3 in Fig. 4). (ii) There were no other obvious differences between the major types of landscapes (1% *vs.* 50% cover) in the distance moved. (iii) There were consistent effects of directionality on these distances across all landscape types. Average ‘birth to death’ distances (both straight line and total) were much longer for high directionality (0.8) than low directionality (0.2) agents. These differences were greater for low percentage cover landscapes (Fig. 4).

Model sensitivity to step length

The average straight-line distance moved over a lifetime was consistently longer for 125-m step length than 50-m step length (Fig. 4). This was an artefact of

the model: larger step lengths mean that monarchs travel further in a straight-line distance than shorter step lengths, when subject to the same directionality parameters. However, the relative differences between landscapes for distances moved are consistent between the two step lengths tested here. Furthermore, the step length has little effect on the number of eggs laid in each habitat type, indicating that the scaling of egg laying rate to step length in the model works well. For the equivalent set of movement parameters, a larger step size (125 m) on average added only 3.4% to the total egg lay so we present detailed results for 50-m step length here for effects on egg laying.

Q2 Egg laying and habitat: landscape resource distribution and the matrix

Habitat preference, landscape and status of the matrix all had an effect on the total eggs laid. Not surprisingly, high landscape cover by habitat (50%) and the status of the matrix had large effects on the total egg laid (Table 3). In landscapes where hosts were present in the matrix, with 50% habitat cover monarch agents laid, on average, 1299 eggs (range 1075–1399) compared to an average of 612 (447–1135) eggs laid in landscapes with 1% cover. The maximum expected fecundity is 1400 eggs. The mean total eggs laid for landscapes with an empty matrix were 1274 (964–1398) and 245 (11–1034) for 50% and 1% cover, respectively. There was a clear interaction between the effect of whether the matrix is empty or not and the percentage cover: there was little effect of an empty matrix when cover is high, but a greater effect when cover is low (Table 3). In the simulation with high cover landscapes, monarch agents did well in terms of eggs laid, regardless of how they move or how resources were arranged. The effects of these other factors became more pronounced in low cover

Table 3. Mean percentage (and range) of eggs laid by 100 monarch agents out of the total possible over a lifetime in each landscape type (range from smallest to largest % eggs for all possible combination of movement parameters) by habitat preference (0.1, 0.5, 1.0)

	Uniform	Fragmented	Clustered	Fragmented	Clustered
Cover %	1	1	1	50	50
Matrix with hosts					
Pref = 0.1	34 (33–35)	32 (31–33)	32 (32–33)	83 (81–84)	80 (75–81)
Pref = 0.5	54 (43–71)	44 (37–55)	37 (32–40)	99 (97–100)	97 (95–99)
Pref = 1.0	67 (49–87)	53 (43–61)	40 (34–56)	100 (99–100)	98 (96–100)
Empty matrix					
Pref = 0.1	3 (2–5)	2 (2–3)	1 (1–2)	80 (78–83)	74 (71–79)
Pref = 0.5	31 (14–55)	19 (10–24)	9 (5–19)	99 (97–100)	97 (91–99)
Pref = 1.0	50 (27–85)	30 (15–68)	13 (5–29)	100 (99–100)	97 (93–100)

The matrix in each landscape either contains a low background density of hosts (matrix with hosts) or is devoid of hosts (empty matrix).

landscapes. We investigated more closely the effect of landscape structure, preference and movement for low cover landscapes below.

Except for the clustered 1% cover landscape with a clean matrix and a low habitat preference value (0.1, highlighted in Table 3), monarch agents did much better than what would be expected by a random search model for an empty matrix situation. For the latter, we would expect that agents would lay eggs in proportion to percentage cover, given they had no preference for either habitat or matrix. In our simulations, they did between 1.5 and 3 times better than a random search model (Table 3).

Unsurprisingly, realized fecundity was higher in landscapes with hosts present in the matrix (compare Fig. 5a and b). Habitat preference has a strong effect on realized lifetime fecundity; as preference increases,

egg number increases for each landscape type, perceptive distance and directionality (Fig. 5ab). Agents had a higher propensity to leave habitat patches when there was no difference between the preferred habitat and matrix preference value (both 0.1) (Fig. 5a) and the eggs per female are low and similar for all these simulations. Monarch agents achieved higher lifetime fecundity in landscapes with a more uniform distribution of habitats (landscape 1) and there was an apparent positive effect of a greater perception distance and a smaller positive effect of directionality for all three landscapes, but it was more apparent in uniform and fragmented landscapes (Fig. 5). Monarch agents did least well in the model landscapes where habitat was clustered (landscape 3).

The distribution of eggs across the landscape (matrix or patches) reflected the presence of adults.

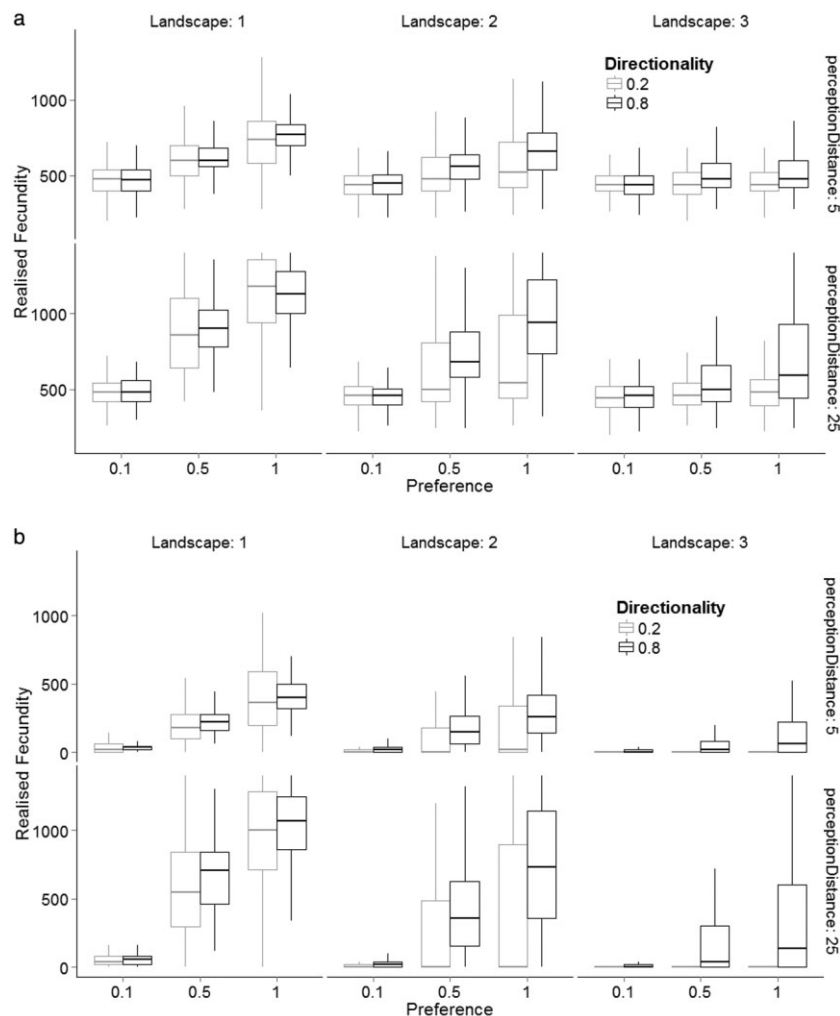


Fig. 5. (a) Box and whiskers plot of realized fecundity per female agent over her lifetime in three landscapes (uniform, fragmented, clustered) with a low habitat cover (1%) for three habitat preference levels (0.1, 0.5, 1.0) for matrix with host plants, top pair of panels (a) and empty matrix, lower pair of panels (b). Effect of perceptive distance; low (5 m) and high (25 m); shown as separate subpanels for each matrix type. Within each perception distance the effect of directionality on realized fecundity; low (0.2) and high (0.8); is shown.

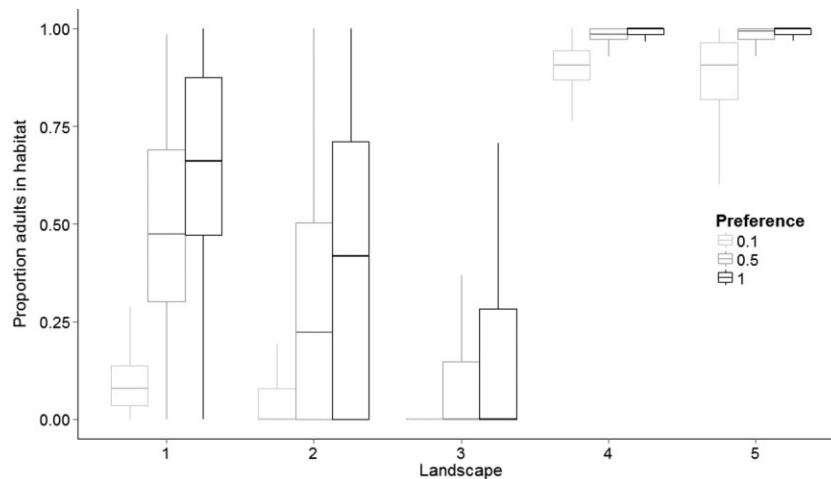


Fig. 6. Box and whiskers plot of the proportion of adults in habitat units (patches) over 14 days for 5 landscape types (see Table 1 for details) and three preference values (0.1, 0.5 and 1). The variation within a landscape type reflects different perception distance and directionality effects.

For low values of habitat preference (0.1) and low percentage habitat cover, most eggs (and thus adults) were not in habitat units (Fig. 6); adults were essentially in the matrix. As preference increased, a higher percentage of eggs (and adults) was found in habitat units in low cover landscapes, but this was much lower than the 80–100% of eggs (and adults) in high cover landscapes (Fig. 6).

Q3 implications for monarch conservation

It has been suggested that to help monarch populations recover, after the desolation of milkweed wrought by Roundup Ready soybean and corn and the concomitant increased use of herbicides, that milkweed be promoted along highways (Fischer *et al.* 2015). For the most favourable low cover landscape (uniform habitat patch distribution) with an empty matrix, analogous to Roundup Ready agriculture in the monarchs summer breeding range in North America (Pleasants & Oberhauser 2012), we added a line of habitat down the middle to mimic the effect of a road with milkweed restored. The addition of this road habitat effectively increased cover from 1 to 2% cover. The gain in egg production averaged 51% (Fig. 7).

DISCUSSION

Time, space and population dynamics revisited

How far do insects fly?

Insects, even small drosophilid, can fly a long way in inhospitable landscapes (Dickenson 2014). From our

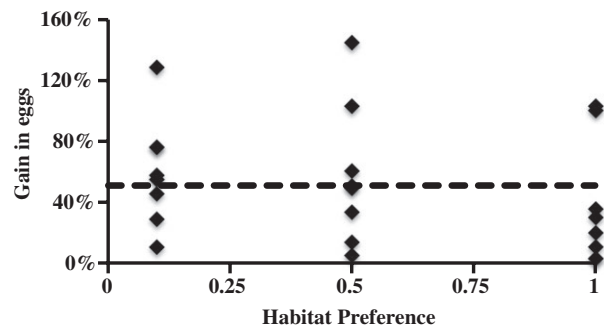


Fig. 7. Gain in eggs for a landscape with a uniform distribution of habitat units to which a road (linear arrangement of habitat) has been added down the middle relative to a uniform landscape (landscape 1 in Table 2) for three habitat preference levels. ‘Gain’ was always measured on comparable model configurations, that is, for the uniform versus line landscape with the same directionality, perception distance, angle, preference, etc. The overall mean gain is shown (dashed line).

behaviour-driven simulations, long movement distances for individual monarch agents emerged under conditions of low habitat availability, particularly when habitat was clustered. This occurred even when undertaking what have been described as ‘trivial’ or foraging movements (Kitching & Zalucki 1982) associated with egg laying (Fig. 4), not the long distance seasonal migrations that population and applied ecologists can consider problematic (e.g. Chapman *et al.* 2003). Our agents were vagile in the sense that even for high habitat preference values relative to the matrix, they still leave. In fact, our preference parameter was best interpreted as a likelihood of leaving a patch. High preference values led to agents concentrating eggs in patches of hosts (cf. Roots’ resource concentration

hypothesis; Root 1972). Butterflies such as the monarch certainly appear to ignore boundaries (Ries & Debinski 2001) and milkweed patch edges (Zalucki & Kitching 1982b) and most likely have low preference levels. These patches essentially define the habitat for this species providing oviposition sites, larval food plants, nectar for adults and mating resources (Bull *et al.* 1985; Zalucki & Kitching 1985; Suzuki & Zalucki 1986; Zalucki 1993). How far such agents will fly, and necessarily the scale at which the 'population' needs to be considered, was a function of landscape features (cover and distribution), relative habitat preference, directionality of movement and step length (Fig. 4). Even for high cover landscapes, movement distances of between 1 and 10 km mean that most populations would be 'open' and not strictly confined to a single patch. For sparse landscapes, the movement distances were potentially much greater (4–20 km) and agree with the 11 km suggested for summer breeding monarchs based on an earlier simulation model (Zalucki 1983). Mark-recapture studies suggested that such movements were common (Zalucki & Kitching 1985). In effect, a 'population' could potentially extend over about 400 km², making population level studies difficult. Such monarch populations could be best described as 'patchy' (*sensu* Thomas & Kunin 1999) not as a so-called 'metapopulation'.

The time honoured method of counting butterflies around patches of food plant habitat (e.g. Pollard 1977; Kemp & Zalucki 1999) might estimate numbers in such patches well but will greatly underestimate 'population abundance'. Most of the adults in sparse habitat cover landscapes (an average of 50–90% depending on habitat preference and habitat distribution) will be 'lost' in the space between habitat patches. These adults may or may not be reproducing, depending on the availability of hosts in the matrix (Shreeve *et al.* 2004) (Fig. 6).

Effects on egg laying

Realized fecundity was greatly influenced by landscape factors, not only by the nature of the matrix but also by how habitat units are arranged, as well as species-specific attributes of habitat preference, perceptive distance and directionality (Fig. 5). As in Zalucki and Lammers (2010), the absence of hosts in the matrix can reduce realized fecundity by up to 30%. Zalucki and Lammers (2010) modelled movement implicitly as a simple searching function. The important difference with the spatially explicit model presented here was that we can now predict egg distributions in specific spatial arrangements of patches as they were an emergent property of the model; potentially a testable hypothesis that we leave to a subsequent paper.

The greater the number of habitat patch units, and the more evenly spaced they were, the more likely they

were to be encountered and utilized. Clustered landscapes, that is where habitats occurred in larger, fewer 'fragments', resulted in the lowest realized fecundity. Apart from directionality (high directionality enabling more patches to be encountered), relative habitat preference and perceptive distance are important. Interestingly, we know very little about either of these 'parameters' for most species.

The search strategies animals use to detect a new habitat when they are 'lost in matrix space' are not well understood (Bowler & Benton 2005). Most studies of movement have focused on the likelihood of leaving a habitat or dispersal propensity (e.g. Schultz & Crone 2001; Berggren *et al.* 2002; Schtickzelle *et al.* 2006). The ability of animals to perceive and locate resources as they move through the landscape will contribute not only to dispersal success in fragmented landscapes, namely finding habitat units (e.g. Merckx & Van Dyck 2007), but also their ability to survive and potentially reproduce in the space or matrix between 'habitat' patches (see the previous discussion). Empirical information on the perceptual abilities of animals in real landscapes is limited (Zollner & Lima 1999; Schooley & Wiens 2003; Merckx & Van Dyck 2007). We know from behavioural and electrophysiological studies that insects can perceive resources, such as host plants, from a distance using odour cues and respond accordingly (e.g. Finch & Collier 2000). However, we have few good estimates of perception distance for host plants, although these seem to be of the order of tens of metres (Cardé & Willis 2008), so our values are likely to be close to correct. These perceptions may be disrupted by many factors and so lead to better or worse localization of resources (Floater & Zalucki 2000; Cardé & Willis 2008). Landscape structure or the nature of the matrix (available resources, physical texture) will also have a direct effect on the movement behaviour of animals, for example, grass-cover permeability (Wiens *et al.* 1997), landscape type (Russell *et al.* 2003) and amount of food present (Wallin & Ekblom 1994).

In our simulations, all resources (hosts, nectar sources, roosting sites) were available in each habitat unit. Should these be heterogeneously distributed requiring additional searching movements, then realized fecundity will be greatly reduced, as posited by Kitching (1977) for blowflies in the section '*Time, space and population dynamics*'.

For monarchs, the suggestion is that realized fecundity has been greatly curtailed due to cleansing of the matrix of host plants. Certainly, there has been a sustained reduction in the size of the overwintering population in Mexico since the advent of Roundup Ready crops. The decline does not seem to contain a strong climate change signal (Zalucki *et al.* 2015), which is often posited as a cause of species decline (e.g. Warren *et al.* 2001).

Conservation: does one size fit all?

Species conservation planning often involves setting aside areas of suitable habitat. Assuming it is not just one large remnant (in which case it should be larger than the 'trivial' foraging distance at least), then how these are best arranged will depend very much on the biology of the species in question. It is unlikely that one arrangement of fragments will equally suit the requirements of all species utilizing such remnant habitats. As the range of results from the simulation model for different combination of movement parameters within one landscape suggest, one size will not fit all. At a minimum, we would need to estimate habitat preference (the propensity to leave), directionality of movement in the space between habitats (the matrix) and how rapidly animals move (step length) as well as perception distance. These would enable better interpretation of data from counts that are almost always undertaken in areas of 'habitat'. As our simulations suggest for some types of animals, most of the adult population will be located away from habitat patches. Putting sentinel plants in non-habitat areas will quickly determine if there is such a floating population, as these plants will be quickly found and exploited (eggs laid) even if adults are not readily seen (see Zalucki & Kitching 1982a), as local density will be low. We would also predict that species with high preference values would have laid most of their eggs at the end of the day, whereas collections of adults with low preference values from patches would have a binomial distribution, consisting of those that have laid their eggs and a few individuals with many eggs to lay (only just arrived at a patch). Such assessments offer indirect ways of studying movement and egg laying in monarchs but would require a way of age grading individuals.

Certainly, aiding the recovery of monarchs could be influenced by the spatial arrangement of milkweed habitat at a landscape scale. A more uniform distribution of habitat units would appear to be more suitable than a few large clusters far apart. Any addition to landscape cover would be helpful and adding milkweed to roads could well increase realized fecundity. Of course, the key question here is would it be sufficient to allow populations to at least replace themselves and persist? That will depend on both the realized fecundity and the survival in patches versus single isolated plants in the matrix (Zalucki & Kitching 1982c). An extension of this simulation modelling approach that includes population dynamics could explore this question in more detail.

CONCLUDING REMARKS

Models are essential tools when attempting to understand ecological processes, such as reproduction, at a

scale relevant to insect population dynamics. Essentially, the conclusion of such modelling follows from the assumptions contained within the model. As McCallum (1995) points out, the leap of faith is that the assumptions adequately describe the 'real' world. The model presented here indicates some credible relationships between the behaviour of monarchs and the likely relative landscape population distribution and realized fecundity: such hypotheses could be tested in the field across a range of landscape types, using a 'model-guided fieldwork' approach *sensu* Restif *et al.* (2012), to see if the emergent patterns suggested by the modelling as a result of underlying processes are valid, thus verifying if our assumptions about these processes are correct. The challenge is to experimentally verify that these agent-based models do in fact capture behaviour and therefore any generated emergent population properties such as 'realized' fecundity is in fact realistic. Or alternatively collect sufficient field data observations to compare patterns of the model outputs with those expected from the field (the pattern-orientated approach).

ACKNOWLEDGEMENTS

Thanks are due to M.P. Zalucki's PhD supervisor, Roger Kitching, for having the foresight to suggest that monarch butterflies were a good model system to study movement and resource use and the temerity to claim everything was known about their biology! We thank Mike Furlong, Cate Paull, Steve Malcolm and Tony Ives for the comments and discussion.

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